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## Failure to Engage Neural Plasticity through Practice of a High-difficulty Task is Accompanied by Reduced Motor Skill Retention in Older Adults

Josje M. Bootsma,<sup>a\*</sup> Simone R. Caljouw,<sup>a</sup> Menno P. Veldman,<sup>b,c</sup> Natasha M. Maurits,<sup>d</sup> John C. Rothwell<sup>e</sup> and Tibor Hortobágyi<sup>a</sup>

<sup>a</sup> Center for Human Movement Sciences, University Medical Center Groningen, University of Groningen, Groningen, The Netherlands

<sup>b</sup> Movement Control and Neuroplasticity Research Group, Department of Movement Science, KU Leuven, Leuven, Belgium

<sup>c</sup> Leuven Brain Institute, Leuven, Belgium

<sup>d</sup> Department of Neurology, University Medical Center Groningen, University of Groningen, Groningen, The Netherlands

<sup>e</sup> Sobell Department of Motor Neuroscience and Movement Disorders, University College London (UCL) Institute of Neurology, London, United Kingdom

**Abstract**—While the difficulty of a motor task can act as a stimulus for learning in younger adults, it is unknown how task difficulty interacts with age-related reductions in motor performance and altered brain activation. We examined the effects of task difficulty on motor performance and used electroencephalography (EEG) to probe task-related brain activation after acquisition and 24-h retention of a mirror star-tracing skill in healthy older adults ( $N = 36$ , 65–86 years). The results showed that the difficulty of the motor skill affected both the magnitude of motor skill learning and the underlying neural mechanisms. Behavioral data revealed that practicing a motor task at a high difficulty level hindered motor skill consolidation. The EEG data indicated that task difficulty modulated changes in brain activation after practice. Specifically, a decrease in task-related alpha power in frontal and parietal electrodes was only present after practice of the skill at the low and medium, but not the high difficulty level. Taken together, our findings show that a failure to engage neural plasticity through practice of a high-difficulty task is accompanied by reduced motor skill retention in older adults. The data help us better understand how older adults learn new motor skills and might have implications for prescribing motor skill practice according to its difficulty in rehabilitation settings. © 2020 The Author(s). Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

**Key words:** aging, EEG, motor learning, plasticity, skill retention, spectral analysis.

### INTRODUCTION

The ability to acquire and retain motor skills facilitates the recovery from injuries caused by orthopedic or neurological conditions and functional independence in old age (Winstein, 1991; Krakauer, 2006). Motor skill learning is the process of practice-dependent improvement of motor performance and emerges as an interplay between motor and cognitive systems (Lee et al., 1994; Krakauer et al., 2019). Practice conditions can affect the effectiveness of motor skill acquisition and the stability

of motor skill retention (Wulf et al., 2010). One particularly important practice condition is the difficulty of the motor task. Yet there is no clear understanding of how task difficulty affects motor skill learning and if it interacts with age-related modifications in motor performance and brain activation. Insights into this interaction could help optimize motor skill learning in older adults and patients recovering from movement impairments.

Without a universal definition, we define motor task difficulty as the level of challenge to execute a motor task within the current spatial and temporal constraints. In younger adults, the performance of increasingly difficult unimanual motor tasks is accompanied by bilateral activation of areas in the sensorimotor and frontoparietal networks (Rietschel et al., 2012; Buetefisch et al., 2014). It has been proposed that increased motor and cognitive demands act as a stimulus for motor learning in young adults up to a point when the available processing capacities are reached (Guadagnoli and Lee, 2004; Akizuki and Ohashi, 2015; Shuggi et al., 2017).

\*Corresponding author. Address: University Medical Center Groningen, Antonius Deusinglaan 1 9713 AV FA23, Groningen, The Netherlands.

E-mail address: [j.m.bootsma@umcg.nl](mailto:j.m.bootsma@umcg.nl) (J. M. Bootsma).

**Abbreviations:** ANOVA, analysis of variance; EEG, electroencephalography; FDR, false discovery rate; NASA-TLX, National Aeronautics and Space Administration Task Load Index questionnaire; P-HD, practice with high difficulty; P-LD, practice with low difficulty; P-MD, practice with medium difficulty; ROI, region of interest; TR-Power, task-related power.

Imaging studies have shown practice-dependent neuroplasticity in sensorimotor and frontoparietal networks after a period of motor practice in young adults, reflected by alterations in the blood oxygenation level-dependent (BOLD) signal as well as oscillatory activity measured with electroencephalography (EEG) (Floyer-Lea and Matthews, 2005; Boonstra et al., 2007; Kranczioch et al., 2008). Oscillations in the alpha and beta frequency ranges are known to be dominant at rest and suppressed during movement (Pfurtscheller and Lopes Da Silva, 1999). After a period of motor practice, several studies have shown a decrease in task-related alpha and beta power, indicative of higher neural activation and associated with early plasticity related to motor learning (Nakano et al., 2013; Gallicchio et al., 2017). If and how practice-related changes in power are modulated by task difficulty is not known yet.

While increased task difficulty could be beneficial for younger adults, it might hinder skill acquisition or retention in older adults whose motor performance and processing capacities are diminished (Light, 1990; Jiménez-Jiménez et al., 2010). Behavioral evidence indeed supports this expectation because the effectiveness of motor learning decreased with increasing task difficulty in older adults (Voelcker-Rehage, 2008; Onushko et al., 2014). Participants who practiced with a low difficulty level of a force coordination task performed better at retention compared to those practicing at a high difficulty level (Onushko et al., 2014). These observations may be explained by bilateral overactivation in older adults when they execute unimanual motor tasks with a relatively low level of difficulty, which could limit additional brain activation that would be needed to execute tasks with a higher level of difficulty (Berghuis et al., 2019; Larivière et al., 2019). However, how task difficulty affects the brain mechanisms of motor learning in older adults remains unexplored.

Motor learning-related neuroimaging data are contradictory in older adults, showing both increases (Rieckmann et al., 2010) and decreases (Berghuis et al., 2019; Espenhahn et al., 2019) in activation in motor-related areas after practice. Age affected alpha and beta power after practice with a complex bimanual coordination task (Rueda-Delgado et al., 2019), but not after practice with a simpler unimanual tracking task (Espenhahn et al., 2019). These contradictory data give rise to the hypothesis that the magnitude of skill acquisition and retention and the related brain activation in older adults varies with the difficulty of the motor task. More specifically, we hypothesized more improvement in motor performance for participants practicing at a lower compared to a high difficulty level of the same task. Furthermore, we expected improvements in motor performance to be accompanied by decreases in power in contralateral sensorimotor areas (Mak et al., 2013; Nakano et al., 2013). Thus, the aim of the current study was to determine for the first time the effects of task difficulty on motor performance, motor skill acquisition, and 24-hour retention, and on associated changes in task-related brain activation in healthy older adults.

## EXPERIMENTAL PROCEDURES

### Participants

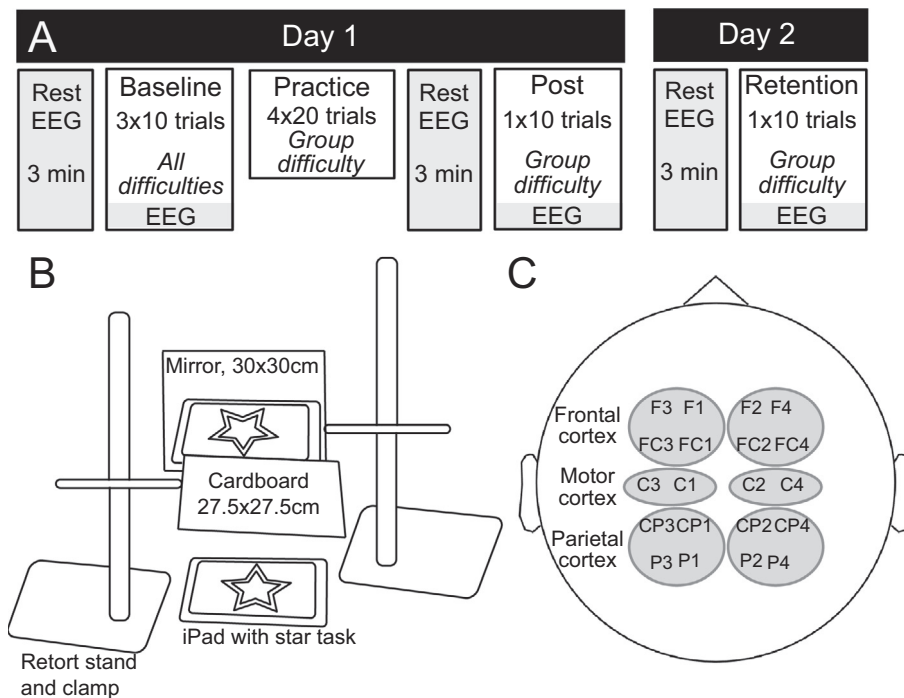
Healthy, right-handed (Oldfield, 1971), community-dwelling older volunteers ( $N = 36$ , age:  $70.4 \pm 4.1$  yr, 20 males) were recruited through advertisements. Participants were physically and cognitively well-functioning, as indicated by the Groningen Activity Restriction Scale ( $18.4 \pm 1.5$ , (Kempen et al., 1996)) and the Mini-Mental State Examination ( $29.2 \pm 1.1$ , (Folstein et al., 1975)). Exclusion criteria were: movement restrictions in the right upper extremity, neurological conditions, and medications affecting neural functioning. Participants were instructed not to consume coffee or tea within one hour before the start of the experiment. Participants gave written informed consent to the study protocol, which was approved by the local ethics committee and the study was conducted in accordance with the Declaration of Helsinki.

### Procedure

Participants visited the lab on two consecutive days and were randomly assigned to one of three difficulty groups. Each group practiced the task at one difficulty level (see below). After a three-minute resting-state EEG measurement, participants were familiarized with the motor task by performing one trial on each of the three difficulty levels (see *Visuomotor task*). Subsequently, they performed ten trials on each difficulty level in a block-randomized order to assess baseline performance, while task-related EEG was recorded. Next, participants practiced the task in four blocks of twenty trials at the assigned difficulty level: Practice (P) with Low, Medium, or High Difficulty (P-LD, P-MD, or P-HD). Practice blocks were separated by five minutes of seated rest. To minimize attentional drift during the practice phase, we conducted the MMSE, the Digit Symbol Substitution subscale of the Wechsler Adult Intelligence Scale III (Wechsler, 1997), and the Brooks Matrix Task (Brooks, 1967) between blocks two and three, and therefore this rest period was longer ( $18 \pm 3$  min). After practice, participants rated the perceived difficulty of the learning task by completing the National Aeronautics and Space Administration Task Load Index questionnaire (NASA-TLX). Finally, EEG was recorded during rest and ten trials of the task at the assigned difficulty level. Participants reported back to the lab after  $24 \pm 2.5$  h for a retention test, including resting-state EEG, motor performance, and task-related EEG measurements. Fig. 1A depicts the study design.

### Visuomotor task

As detailed previously (Bootsma et al., 2018), we measured motor skill performance in a mirror star-tracing task on a  $28 \times 21.5$  cm Apple iPad Pro (Fig. 1B). Participants sat in a comfortable chair in front of a table. The iPad was placed on the table-top and vision of the iPad was blocked by a sheet of cardboard placed horizontally above the iPad. Participants were only able to see the symmetrical five-point star and their moving hand through



**Fig. 1.** (A) Experimental design of the study. Resting-state EEG, task-related EEG and motor performance measures were taken before, immediately after and 24 h after motor practice. (B) Participants were asked to trace the outline of a star as fast and accurately as possible, while only allowed to look at their moving hand through a mirror. (C) A topographical plot showing the location of the combination of electrodes used for the regions of interest.

a mirror placed vertically behind the iPad. The length of each of the five sides of the star was 10.5 cm and task difficulty was manipulated by changing the width of the pathway to respectively 7 (Low Difficulty, LD), 5 (Medium Difficulty, MD) or 3 mm (High Difficulty, HD), i.e., an increase of the spatial constraints. Participants were instructed to stay within the width of the pathway and trace the star as quickly and accurately as possible in a counter-clockwise direction with an Apple Pencil held in the right hand. Participants started a trial by placing the stylus on a blue dot and finished it by returning to this blue dot after tracing the pathway of the star. The sound of a beep signaled to start tracing. Between two consecutive trials, the screen turned black and refreshed with the appearance of the next star template. In the practice phase, the movement time and bandwidth error (see *Data analysis*) appeared on the screen after every trial to provide participants with feedback about their performance.

### NASA-TLX

The NASA-TLX is a valid, self-reported measure of perceived mental workload, including the subscales of mental demand, physical demand, temporal demand, performance, effort, and frustration (Hart and Staveland, 1988). We validated a Dutch translation of the NASA-TLX using backward translation (Beaton et al., 2000; Supplementary Table S1). Participants rated the perceived demand of the practiced difficulty level from 0 to 100 on each subscale. A Raw Task Load Index was obtained by averaging the six subscale scores (Byers et al., 1989).

### EEG recording

EEG data were acquired in a shielded room using a Brainvision actiCHamp active electrode system and recorded using the BrainVision Recorder software (Brain Products GmbH, Germany). The active Ag/AgCl electrodes were placed in a 64-channel electrode cap according to the international 10–10 system (Chatrian et al., 1985). The impedance of all electrodes was kept below 10 k $\Omega$  using conductive gel (SuperVisc-Gel, EasyCap, Germany). The ground electrode was placed between Fp1 and Fp2 and the Fz electrode was used as the recording reference. Raw resting-state and task-related EEG data were continuously recorded at 250 Hz. For the resting-state measurements, participants were asked to try and avoid movements and blinking, while keeping their eyes open for three minutes. During task execution, the start and end of each trial were automatically marked in the continuous EEG recording. The data were stored on a personal computer for offline analysis.

### Data analysis

Visuomotor and EEG data were exported and analyzed using custom-made Matlab scripts (The Mathworks, Natick, MA; version R2018b).

**Motor performance.** Position data were exported from the iPad and interpolated at 60 Hz. To exclude errors participants made due to the start and end of a trial, the first and last line segments of the star were excluded from the analysis (2/10 total line segments). Motor performance was quantified in terms of both speed (movement time) and accuracy (bandwidth error). We calculated movement time as the duration of the total trial time (i.e., the time it took participants to complete the truncated path of the star one time), while bandwidth error was calculated as the percentage of a trial that participants spent outside of the pathway. Both scores were then averaged over the ten trials of each test. Because initial learning is very rapid in this form of the star tracing task and to fully capture the effects of task difficulty, we established pre-test motor performance from the first ten practice trials instead of the trials during the baseline test.

**EEG data preprocessing.** The Fieldtrip Toolbox was used for the preprocessing and analysis of EEG data (Oostenveld et al., 2011). Raw EEG data were low-pass

filtered (4th order Butterworth, 70 Hz), band-stop filtered at 50 Hz to remove line-noise, and re-referenced with an average reference. Channels with bad signal were visually identified and removed before re-referencing. Subsequently, we extracted the EEG data that were recorded while participants performed the task. Similar to the behavioral analysis, the first and last 10% of the data of each trial were discarded before segmenting. Pre-test EEG data were obtained from the trials of the baseline test that were performed on the difficulty level participants subsequently practiced with. Resting-state and task-related data were then segmented into non-overlapping 1-s-long epochs. After epoching, the data were upsampled to 256 Hz using piecewise cubic interpolation to aid the calculation of the power spectra and visually checked for artifacts. An independent component analysis was applied and components containing eye blinks or movement artifacts were identified and removed from the data (Delorme et al., 2007). Lastly, Fieldtrip's summary function was used to discard epochs in which the maximum absolute value exceeded 100  $\mu\text{V}$  or the kurtosis was greater than 10.

**EEG data analysis.** Power spectra from clean epoched EEG data were calculated using a Fast Fourier Transform with a 10% Hanning window, resulting in a frequency resolution of 1 Hz. Power values were averaged over the alpha (8–12 Hz) and beta (12–30 Hz) frequency bands. Regions of interest (ROIs) over the frontoparietal and sensorimotor networks were defined based on previous literature (Serrien and Brown, 2003; Veldman et al., 2018; Rueda-Delgado et al., 2019). Specifically, we determined oscillatory activity over the contra- and ipsilateral frontal cortex (contralateral: average of F3, FC3, F1, and FC1; ipsilateral: average of F4, FC4, F2, and FC2), motor cortex (contralateral: average of C3 and C1; ipsilateral: average of C4 and C2) and parietal cortex (contralateral: average of CP3, P3, CP1, and P1; ipsilateral: average of CP3, P3, CP2, and P2). A combination of specific electrodes was used as a representation of activity in the listed areas (Fig. 1C). In the remainder of the paper, we will use the names of these areas for readability. To reduce inter-individual variability, task-related power values (TR-Power) were calculated as a percentage of power change during task execution ( $\text{Power}_{\text{task}}$ ) relative to power during the resting-state measurement ( $\text{Power}_{\text{rest}}$ ) according to the following equation:

$$\text{TR - Power} = \frac{\text{Power}_{\text{task}} - \text{Power}_{\text{rest}}}{\text{Power}_{\text{rest}}} \times 100 \quad (1)$$

For each session, TR-Power was calculated relative to the resting-state power from that specific session. Calculated this way, a decrease in TR-Power can be considered as an index of higher neural activity (Pfurtscheller and Lopes Da Silva, 1999).

### Statistical analyses

Data were checked for normality with the Shapiro-Wilk test and homogeneity of variances using Levene test (SPSS, v26, IBM). Movement time and bandwidth error were non-normally distributed and therefore transformed

using a log-transformation. Results are reported untransformed as mean  $\pm$  SD. The assumption of homogeneity of variances was met for all variables. For TR-Power, outliers were defined as average ROI values larger than two SDs above the group mean for each frequency band, area, and session separately and removed from further analysis (8.8% of total data points). In addition, retention test data from two subjects were missing for technical reasons. Separate one-way ANOVAs were performed to assess differences between difficulty groups in participant characteristics and NASA-TLX ratings. Effect sizes were calculated as partial eta squared ( $\eta_p^2$ ).

Behavioral and EEG power data were analyzed with multilevel analysis using MLwiN version 3 (Center for Multilevel Modeling, University of Bristol, Bristol, UK). Multilevel analysis acknowledges the hierarchical structure of the data and is robust to missing values (Quené and Van Den Bergh, 2004). The deviance ( $-2 * \log\text{-likelihood}$ ) of the models, which are specified below, was compared using a  $\chi^2$  test to evaluate model fit. In the case of significant main effects, Z-scores were calculated from the relevant predicted coefficients as post-hoc comparisons. Within each model, the probabilities for coefficients and post-hoc comparisons were corrected for multiple testing using a false discovery rate (FDR) correction. Because interaction effects are difficult to interpret directly from the models, significant difficulty  $\times$  time interactions were investigated further with a Tukey's HSD post-hoc test.

**Behavioral models.** First, linear random slope and intercept models (model 1) were constructed for both motor performance outcomes (movement time and bandwidth error) where repeated measures (level 1) were nested within subjects (level 2). For the baseline phase, repeated measures consisted of all three difficulty conditions. To assess the effect of task difficulty on motor performance, difficulty condition (LD, MD, HD) was added to the model as a factorial predictor (model 2). In addition, model 2 also contained the factorial predictors difficulty group (P-LD, P-MD, P-HD), to examine potential baseline differences between groups, and block (block 1, block 2, block 3), to assess fast initial learning during the baseline phase. Changes in motor performance outcomes over time were examined with separate multilevel models, where pre, post, and retention time-points served as repeated measures (level 1). Time (pre, post, and retention) and difficulty group (P-LD, P-MD, P-HD) were added to the models as factorial predictors (model 2). Subsequently, to test the hypothesis that changes over time are dependent on task difficulty, difficulty group  $\times$  time interactions were added as predictors to the models (model 3).

**EEG models.** Separate linear random slope and intercept models were constructed to assess changes in TR-Power for each frequency band and each area (model 1). Again, models were constructed for the baseline and practice phases separately. For the

baseline phase, in model 2 the factorial predictors difficulty condition (LD, MD, HD), hemisphere (contralateral, ipsilateral), and difficulty group (P-LD, P-MD, P-HD) were added. Next, to test if task difficulty affected TR-Power differently for the contra- compared to the ipsilateral hemisphere, difficulty condition  $\times$  hemisphere interactions were added to the models as predictors (model 3). For the practice phase, the factorial predictors time (baseline, post, and retention), difficulty group (P-LD, P-MD, P-HD), and hemisphere (contralateral, ipsilateral) were added to the models (model 2). Besides the difficulty group  $\times$  time interactions, model 3 for the practice phase also included difficulty group  $\times$  hemisphere, time  $\times$  hemisphere, and difficulty group  $\times$  time  $\times$  hemisphere interactions as predictors.

**Correlation analysis.** Finally, we performed Pearson's correlation analysis to assess the relationship between motor performance and TR-Power. Exploratory analyses revealed that correlation coefficients did not differ between the different areas and hemispheres. Therefore, whole-brain averages were computed and used for the subsequent correlation analysis to reduce the number of comparisons. Correlations were calculated separately for baseline, post, and retention time-points, as well as for the two frequency bands (alpha, beta). Furthermore, Pearson's correlations were computed between improvement in motor performance and changes in TR-Power, to see if motor skill acquisition and retention was related to changes in oscillatory activity. Changes in motor performance were calculated as the absolute improvement relative to the pre-test, so that positive scores reflect improvement in motor performance, while absolute changes in TR-Power were calculated by subtracting pre-test values from respectively the post- and retention values. An FDR correction was applied to correct for multiple comparisons. For all analyses, the significance level was set at  $\alpha = 0.05$ .

## RESULTS

Difficulty groups did not differ in age, height, weight, and cognitive or physical function. A one-way ANOVA on

perceived mental workload revealed no main effect of difficulty (Table 1).

### Task difficulty affects accuracy, but not speed of skill execution at baseline

At baseline, there were no differences between difficulty conditions in movement time in the whole sample ( $\chi^2_2 = 3.4$ ,  $p = 0.18$ ; Fig. 2A), but there was, as expected, a main effect of difficulty condition for bandwidth error ( $\chi^2_2 = 72.4$ ,  $p < 0.001$ ; Fig. 2B; supplementary table S2). Inspection of contrasts revealed that bandwidth error differed between the three difficulty conditions, confirming the successful manipulation of task difficulty (P-LD vs. P-MD:  $Z = 6.9$ , P-LD vs. P-HD:  $Z = 12.4$ , P-MD vs. P-HD:  $Z = 5.5$ ; all  $p < 0.001$ ). In addition, the addition of block as a factorial predictor significantly improved the model for both outcome measures (movement time:  $\chi^2_2 = 76.7$ ,  $p < 0.001$ ; bandwidth error:  $\chi^2_2 = 14.4$ ,  $p < 0.001$ ), indicating rapid initial learning during the baseline phase (movement time:  $18.7 \pm 13.9$  s improvement block 1 to block 3,  $Z = 11.4$ ,  $p < 0.001$ ; bandwidth error:  $7.7 \pm 21.3\%$  improvement block 1 to block 3,  $Z = 4.1$ ,  $p < 0.001$ ). Difficulty group did not improve the models for any outcome measure, indicating no baseline differences between the three practice groups (movement time:  $\chi^2_2 = 2.7$ ,  $p = 0.18$ ; bandwidth error:  $\chi^2_2 = 1.9$ ,  $p = 0.38$ ).

### Task difficulty affects skill learning

Fig. 3 shows the motor performance of the three groups over the time-course of the experiment. Results of the multilevel models are summarized in Supplementary table S3. There was significant variance within (level 1; movement time:  $Z = 5.5$ ; bandwidth error:  $Z = 5.4$ ; both  $p < 0.001$ ) and between (level 2; movement time:  $Z = 3.8$ ; bandwidth error:  $Z = 4.0$ ; both  $p < 0.001$ ) subjects for both movement time and bandwidth error (variance partition

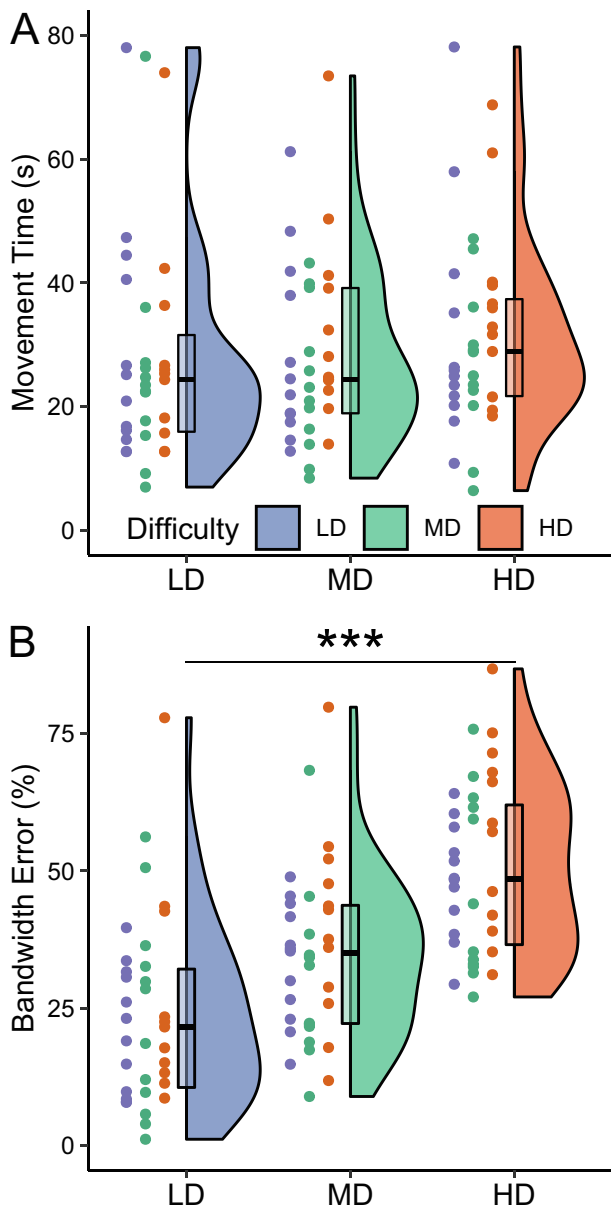
coefficient: 67.6% and 83.9% respectively), justifying the use of multilevel analysis for the behavioral data.

**Speed.** Practice of the motor task, as well as its difficulty, affected movement time. Adding the factorial predictors time and difficulty group to the random slope and intercept model (model 1) improved the model

**Table 1.** Participant characteristics.

	P-LD <i>N</i> = 12	P-MD <i>N</i> = 12	P-HD <i>N</i> = 12	Between-difficulty difference		
				Test statistic	$\eta^2_p$	<i>p</i>
Sex (M/F)	7/5	7/5	6/6	$\chi^2_2 = 0.22$	–	0.90
Age (y)	70.3 $\pm$ 3.2	69.8 $\pm$ 3	71 $\pm$ 5.7	$F_{2,33} = 0.27$	0.016	0.76
Height (cm)	173 $\pm$ 8.9	173.1 $\pm$ 9.9	175.2 $\pm$ 7.5	$F_{2,32} = 0.22$	0.014	0.80
Weight (kg)	84.3 $\pm$ 20.5	78 $\pm$ 12.7	70 $\pm$ 9	$F_{2,32} = 2.6$	0.14	0.09
MMSE	29.3 $\pm$ 1	29.4 $\pm$ 0.9	28.8 $\pm$ 1.4	$F_{2,33} = 0.96$	0.055	0.4
GARS	18.7 $\pm$ 2	18 $\pm$ 0	18.6 $\pm$ 1.5	$F_{2,33} = 0.67$	0.039	0.52
R-TLX	40.4 $\pm$ 19.4	47.9 $\pm$ 12.0	50.2 $\pm$ 22.7	$F_{2,32} = 0.93$	0.053	0.41

Values are presented as mean  $\pm$  standard deviations. *P-LD*: Practice with Low-Difficulty Task, *P-MD*: Practice with Medium-Difficulty Task, *P-HD*: Practice with High-Difficulty Task; *MMSE*: Mini-Mental State examination ( $> 26$  cognitively healthy), *GARS*: Groningen Activity Restriction Scale (18–72, higher scores means more restrictions with ADL activities), *R-TLX*: Raw Task Load Index, as measured with the NASA-TLX questionnaire.



**Fig. 2.** Raincloud plots of the effects of task difficulty (LD, MD, HD) on motor performance measured by movement time (**A**) and bandwidth error (**B**) at baseline. Violin plots at the right show the probability density, the box-plot in the middle represents the median and interquartile range and dots on the left represent the individual raw data of the P-LD (blue), P-MD (green) and P-HD (orange) difficulty groups respectively. \*\*\*Main effect of difficulty at  $p < 0.001$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(model 2, main effect of time:  $\chi^2_2 = 29.7$ ,  $p < 0.001$ , main effect of difficulty group:  $\chi^2_2 = 7.8$ ,  $p = 0.02$ ). Inspection of the main effect of time revealed that although movement time improved by 27.1% from pre to post ( $Z = 5.9$ ,  $p < 0.001$ ), this improvement was not maintained at retention (movement time increased 20.9% post to retention,  $Z = 4.3$ ,  $p < 0.001$ ; Fig. 3A). The main effect of difficulty group indicated that over all time points, P-LD moved 36.9% faster compared to P-HD ( $Z = 2.8$ ,

$p = 0.007$ ). The difficulty group  $\times$  time interaction did not improve the model (model 3,  $\chi^2_4 = 4.4$ ,  $p = 0.36$ ).

**Accuracy.** Bandwidth error decreased over practice and differed between difficulty groups, as the addition of time ( $\chi^2_2 = 18.05$ ,  $p < 0.001$ ) and difficulty group ( $\chi^2_2 = 23.7$ ,  $p < 0.001$ ) to the random slope and intercept model (model 1) improved the model (model 2). In contrast to improvements in speed, improvements in accuracy from pre to post (18.9%;  $Z = 4.1$ ,  $p < 0.001$ ) were maintained at retention (18.1% difference pre to retention;  $Z = 3.8$ ,  $p < 0.001$ ; Fig. 3B). Post-hoc inspection of the main effect of difficulty group revealed that P-LD moved more accurately than both P-MD (69.1% difference,  $Z = 2.04$ ,  $p = 0.04$ ) and P-HD (116.6% difference,  $Z = 5.7$ ,  $p < 0.001$ ), and P-MD moved more accurately than P-HD (59.5% difference,  $Z = 3.6$ ,  $p < 0.001$ ). The difficulty group  $\times$  time interaction further improved the model (model 3,  $\chi^2_4 = 9.8$ ,  $p = 0.043$ ). While bandwidth error decreased from post to retention in P-LD (8.2%,  $p < 0.001$ ) and P-MD (5.8%,  $p < 0.001$ ), it increased by 6.7% from post to retention in P-HD ( $p > 0.05$ ; Fig. 3B). In summary, while participants improved both speed and accuracy immediately after practice, only improvements in accuracy were maintained at retention. Furthermore, task difficulty affected the consolidation of bandwidth error.

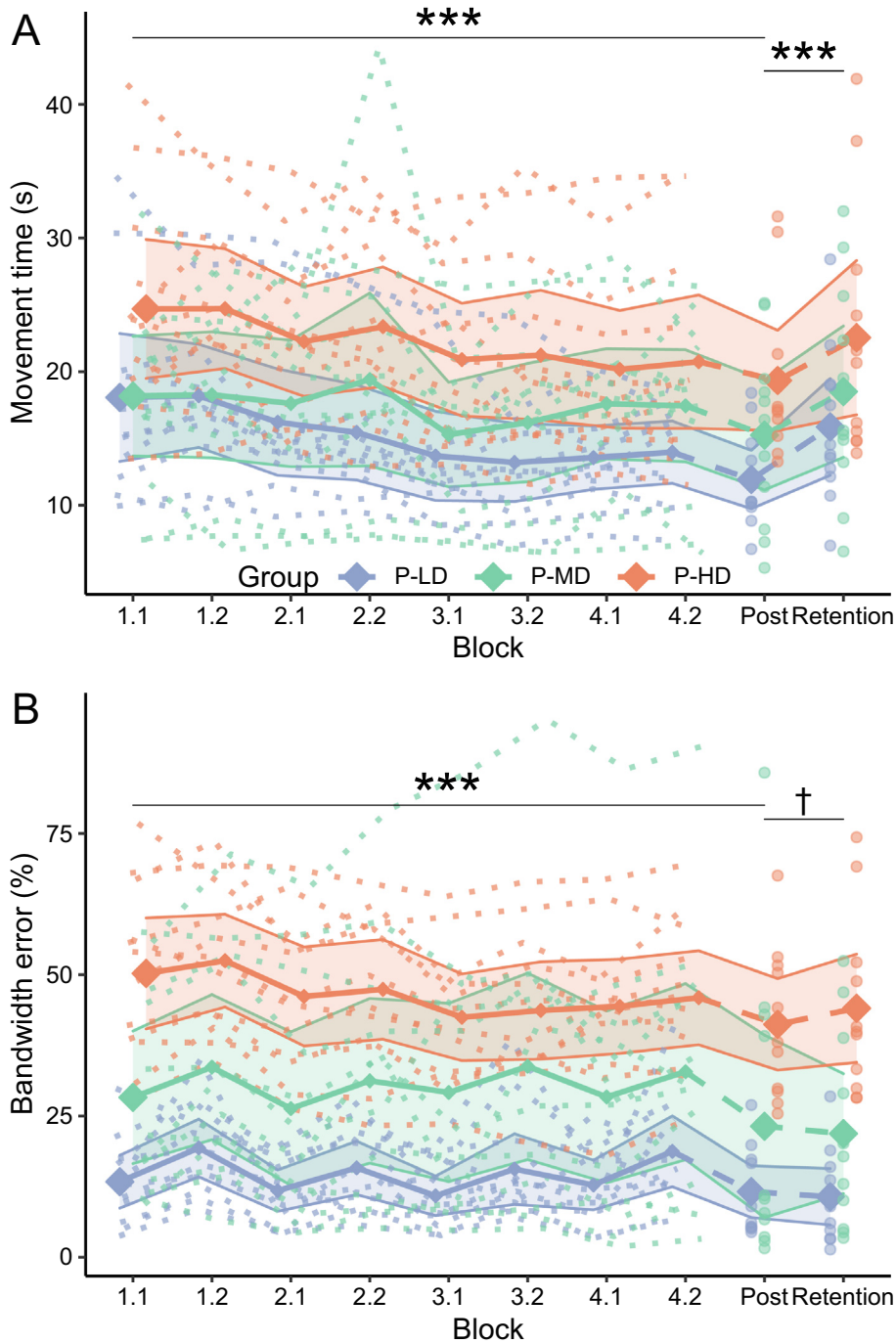
#### Task difficulty does not affect task-related power at baseline

Difficulty condition did not affect TR-Power during the baseline phase in any of the frequency bands or areas (supplementary table S4). Addition of the factorial predictor hemisphere improved the model for alpha TR-Power in the motor cortex ( $\chi^2_1 = 6.6$ ,  $p = 0.01$ ) and beta TR-Power in the frontal cortex ( $\chi^2_1 = 3.9$ ,  $p = 0.049$ ). For both cortices, TR-Power was lower (i.e. higher neural activity) in the ipsi- compared to the contralateral hemispheres. Furthermore, there was a main effect of block only for beta TR-Power in the motor cortex ( $\chi^2_2 = 6.5$ ,  $p = 0.04$ ). In this area, beta TR-Power increased from block 1 to block 3 of the baseline phase (6.7%,  $Z = 2.5$ ,  $p = 0.048$ ). Addition of difficulty group and the difficulty condition  $\times$  hemisphere interaction did not improve any of the models.

#### Decrease in task-related power after practice depends on task difficulty

All TR-Power variables showed significant level 1 and level 2 variance, with variance partition coefficients ranging from 56.6 to 77.6%. Figs. 4–5 and Supplementary table S5 summarize the multilevel models for TR-Power.

**Alpha band.** Practice of the motor task altered TR-Power in the alpha band across the whole brain, as addition of time to the random slope and intercept models (model 1) improved the models for all areas (model 2; frontal:  $\chi^2_2 = 7.7$ ,  $p = 0.022$ ; motor:  $\chi^2_2 = 17.5$ ,  $p < 0.001$ ; parietal:  $\chi^2_2 = 16.9$ ,  $p < 0.001$ ; Fig. 4).



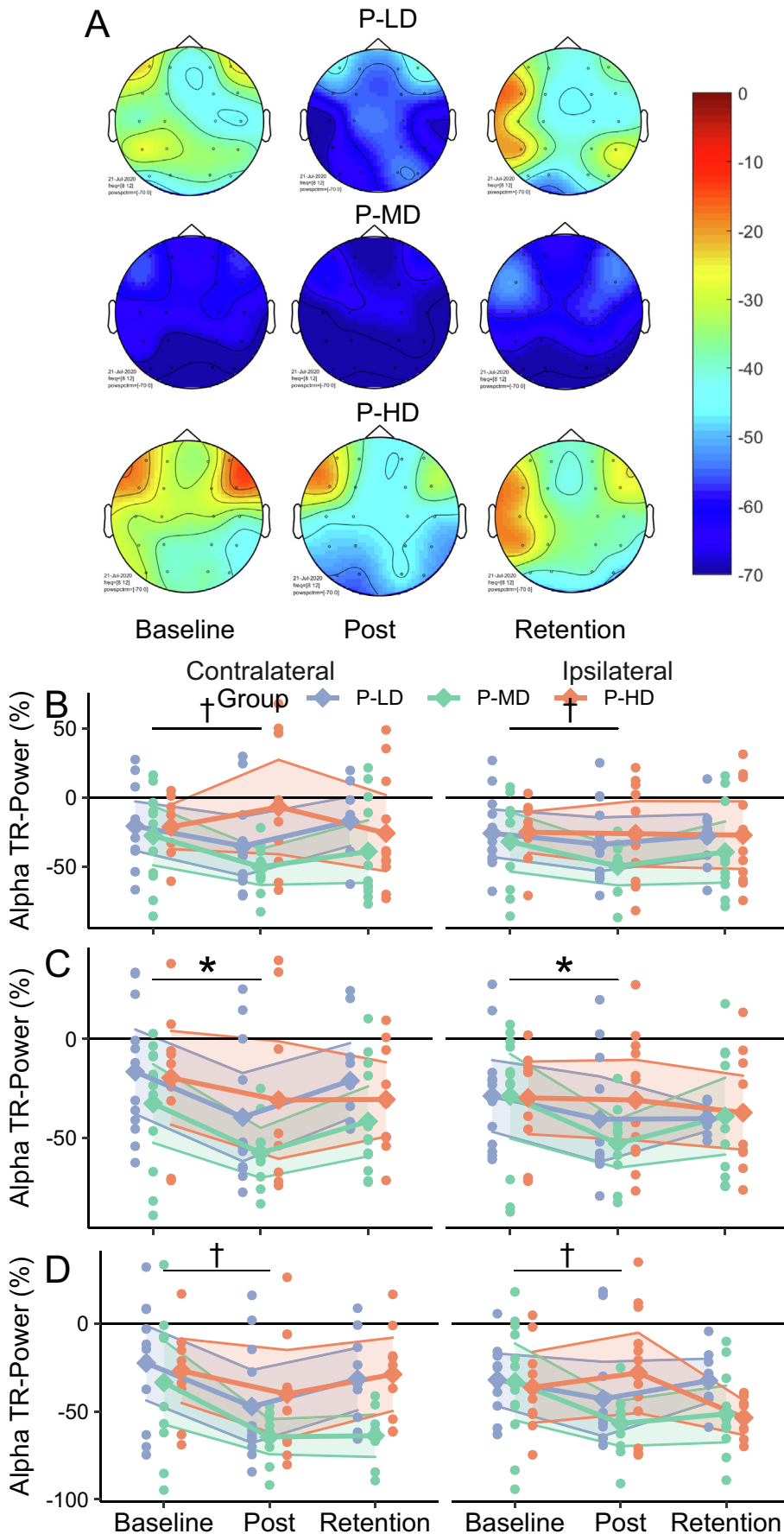
**Fig. 3.** Mean motor performance during, immediately after (Post) and 24 h after (Retention) the motor practice phase for P-LD (blue), P-MD (green) and P-HD (orange), as quantified by Movement Time (A) and Bandwidth Error (B). Big diamonds are representative of time-points used for statistical analysis. Shaded areas represent the 95% confidence interval and lines and dots in the background denote trajectories from individual participants. \*\*\*Main effect of time at  $p < 0.001$ ; †Time  $\times$  Group interaction at  $p < 0.05$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Inspection of the coefficients revealed that TR-Power in the alpha band decreased with 31.4–47.2% from baseline to post at all areas in both hemispheres (frontal:  $Z = -2.8$ ,  $p = 0.005$ ; motor:  $Z = -4.3$ ,  $p < 0.001$ , parietal:  $Z = -4.2$ ,  $p < 0.001$ ) and reverted to baseline levels at 24-h retention (11.8–19.1% difference post-retention;

frontal:  $Z = 1.4$ ,  $p = 0.16$ ; motor:  $Z = 2.2$ ,  $p = 0.025$ ; parietal:  $Z = 2.5$ ,  $p = 0.012$ ). There were no main effects of difficulty group (model 2; frontal:  $\chi^2_2 = 2.8$ ,  $p = 0.25$ ; motor:  $\chi^2_2 = 2.7$ ,  $p = 0.26$ ; parietal:  $\chi^2_2 = 4.4$ ,  $p = 0.11$ ) or hemisphere (model 2; frontal:  $\chi^2_1 = 1.04$ ,  $p = 0.31$ ; motor:  $\chi^2_1 = 2.0$ ,  $p = 0.16$ ; parietal:  $\chi^2_1 = 0.05$ ,  $p = 0.82$ ). However, for the frontal and parietal cortices, addition of the difficulty group  $\times$  time interaction improved the models (model 3; frontal:  $\chi^2_4 = 9.97$ ,  $p = 0.041$ ; parietal:  $\chi^2_4 = 11.2$ ,  $p = 0.024$ ). In these areas, the reduction in TR-Power from baseline to post was only present in P-LD (frontal: 38.9% decrease baseline-post, parietal: 40.7% decrease baseline-post, both  $p < 0.05$ ) and P-MD (frontal: 53.9% decrease baseline-post, parietal: 57.5% decrease baseline-post, both  $p < 0.05$ ), while TR-Power did not change over time in P-HD (frontal: 16.6% increase baseline-post, parietal: 26.6% decrease baseline-post, both  $p > 0.05$ ). All other interactions did not further improve the models. Thus, the results showed a decrease in alpha TR-Power (i.e. increased neural activity) from baseline to post in all areas. Frontal and parietal alpha power only decreased in P-LD and P-MD, while it remained unchanged in P-HD.

**Beta band.** Similar to changes in the alpha band, practice induced changes in TR-Power across the whole brain in the beta band. The addition of time to the random slope and intercept models (model 1) improved the models for all areas (model 2; frontal:  $\chi^2_2 = 10.4$ ,  $p = 0.006$ ; motor:  $\chi^2_2 = 27.7$ ,  $p < 0.001$ ; parietal:  $\chi^2_2 = 16.04$ ,  $p < 0.001$ ; Fig. 5). Post-hoc inspection of the coefficients showed that TR-Power in the beta band decreased 29.3–60.2% immediately after practice in all areas and in both hemispheres (frontal:  $Z = -3.2$ ,  $p = 0.0014$ ; motor:  $Z = -4.5$ ,  $p < 0.001$ , parietal:  $Z = -2.9$ ;  $p = 0.0019$ ) and returned to baseline levels at 24-h retention (23.3–42.3% difference post-retention; frontal:  $Z = 1.9$ ,  $p = 0.057$ , motor:  $Z = 5.0$ ,  $p < 0.001$ ;





parietal:  $Z = 4.0$ ,  $p < 0.001$ ). There were no main effects of difficulty group (model 2; frontal:  $\chi^2_2 = 4.6$ ,  $p = 0.1$ ; motor:  $\chi^2_2 = 1.9$ ,  $p = 0.39$ ; parietal:  $\chi^2_2 = 1.5$ ,  $p = 0.47$ ) or hemisphere (model 2; frontal:  $\chi^2_1 = 1.8$ ,  $p = 0.18$ ; motor:  $\chi^2_1 = 3.5$ ,  $p = 0.06$ ; parietal:  $\chi^2_1 = 3.5$ ,  $p = 0.06$ ). For the motor area, the hemisphere  $\times$  time interaction did improve the model ( $\chi^2_2 = 9.06$ ,  $p = 0.01$ ). In this area, the reduction in TR-Power from baseline to post was only present in the contralateral hemisphere (64.03% decrease baseline-post,  $Z = 5$ ,  $p < 0.001$ ), while TR-Power did not change over time in the ipsilateral hemisphere (8.7% decrease baseline-post,  $Z = 1.4$ ,  $p = 0.16$ ). All other interactions did not further improve the models. Taken together, beta TR-Power decreased (i.e. increased neural activity) from baseline to post in all areas except the ipsilateral motor cortex, with no differences between difficulty groups.

**Correlation analysis**

No correlations were found between motor performance and TR-power at any time-point (Supplementary table S6). Improvements in motor performance also did not correlate with changes in TR-Power (Supplementary table S7).

**DISCUSSION**

The current study is the first to examine the effects of task difficulty on motor skill learning and task-related measures of brain activity in healthy older adults. In agreement with the hypothesis, both motor skill consolidation and changes in brain activation over a single motor practice session varied between groups that practiced the skill at different difficulty levels. Behaviorally, speed and accuracy measures improved pre- to post-training in all groups. In addition, improvements in accuracy, but not speed, became consolidated into memory, as evidenced by performance stabilization at the 24-h retention test. These consolidation effects were modulated by difficulty of the practice condition because accuracy at 24-h retention relative to

pre-training was worse in P-HD compared to P-LD and P-MD. On the neural level, there was a decrease of alpha and beta TR-Power (i.e., higher neural activity) immediately, but not 24-h after motor practice. The decrease in alpha TR-Power in the frontal and parietal cortices during skill acquisition was dependent on task difficulty, as it was only present in P-LD and P-MD. Together, these findings suggest that a failure to engage neural plasticity through practice of a high-difficulty task is accompanied by reduced motor skill retention in older adults.

### Motor skill retention, but not acquisition is related to task difficulty

We manipulated the difficulty of the motor skill by changing the spatial constraints of the task. As expected, this manipulation affected the accuracy of skill execution, as evidenced by an increase in bandwidth error with increased task difficulty during the baseline phase. However, the speed of skill execution was not affected by task difficulty at baseline. Because the order of task difficulty conditions during baseline was block randomized between participants, the effects of task difficulty on motor speed might have been masked by the rapid improvement we observed over the three blocks of the baseline phase. Fast initial learning of a mirror star tracing task is consistent with a previous study in younger adults and can be explained as a transient warm-up effect (Joseph et al., 2013).

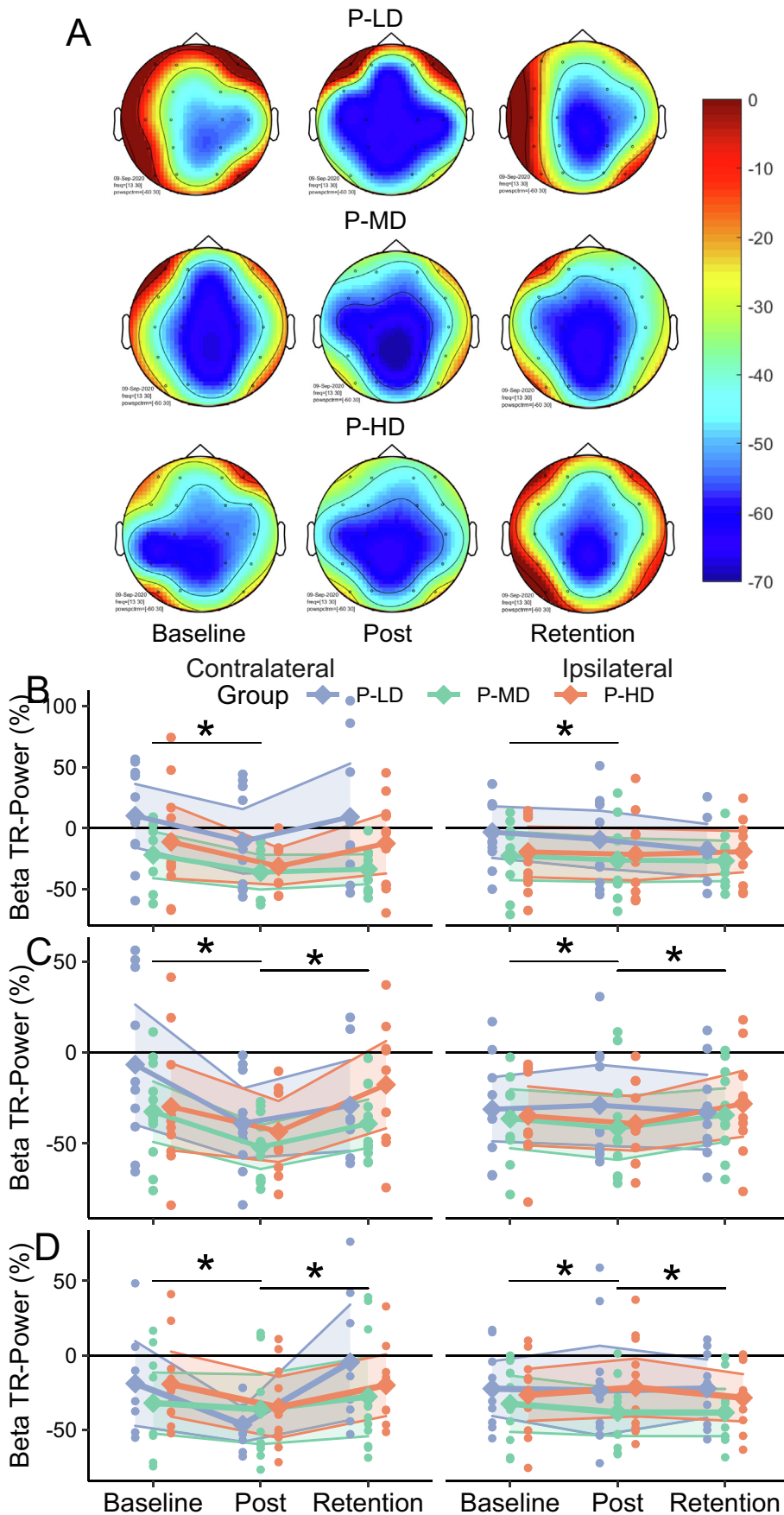
We hypothesized that by reducing the width of the pathway, participants would be forced to control their movements more precisely, increasing motor and cognitive demands. In young adults, these increased demands are known to affect skill acquisition (Guadagnoli and Lee, 2004; Lee et al., 2016; Raw et al., 2019). Even though task difficulty affected overall performance speed and accuracy, it did not impact the magnitude of pre-to-post skill acquisition in the current sample of healthy older adults. Similarly, we found no effects of task difficulty on perceived mental workload. A possible explanation could be that participants adopted a compensatory strategy that slowed movement execution in the high difficulty task (Fig. 2A). Movement slowing to execute difficult motor tasks is a well-reported phenomenon in older adults to counteract age-typical changes in motor variability and processing speed (Rodrigue et al., 2005; Lamb et al., 2016) and was also previously reported in younger adults using the same task (Bootsma et al.,

2018). Thus, the current data suggest that older adults were able to successfully compensate for the increase in task difficulty in the mirror star-tracing task as used in the present study, and were, therefore, able to improve during the skill acquisition phase.

While the pattern of change within the practice phase was not the main interest of the current study, the pattern of data in Fig. 3 is worth mentioning. Performance improved over the entire practice phase of four blocks, yet Fig. 3B reveals that within a practice block bandwidth error deteriorated (e.g. from 1.1. to 1.2, from 2.1. to 2.2, etc.), and also movement time seems to deteriorate within practice block 2 (i.e. from 2.1. to 2.2). Inspection of the pattern in Fig. 3 reveals that improvements in performance predominantly occurs between blocks, where participants had a little rest period of five minutes. The performance improvement between blocks may therefore point to a rapid form of consolidation. The same pattern has recently been reported during early skill acquisition of a sequential key pressing task in younger adults, where all early learning was accounted for by performance improvements during rest periods rather than improvements during practice periods (Bönstrup et al., 2019). The authors interpreted this finding as a rapid form of consolidation possibly arising from the unmasking of inhibitory effects like fatigue (Bönstrup et al., 2019). The current results suggest that rapid offline consolidation may be responsible for motor skill acquisition not only in younger but also in older adults. However, the changes in the practice phase were not amenable to statistical analyses and therefore, no formal conclusions can be made.

Interestingly, improvements in speed were not retained 24-h after practice at any difficulty condition. While it is known that older adults often sacrifice speed to maintain accuracy (Lamb et al., 2016), a lack of correlation between movement time and bandwidth error at the retention test ( $r = 0.046$ ,  $p = 0.79$ ) supports the idea that the two outcomes measure different features of the skill. Furthermore, while participants who practiced at low and medium difficulty showed stabilization in bandwidth error at 24-h retention, bandwidth error increased between the post and retention test for participants who practiced at high difficulty. Impaired learning of tasks with a high level of difficulty in older adults is in line with earlier research and could be explained by the optimal challenge point framework, which states that tasks that are too difficult might overwhelm the performer and interfere with learning (Guadagnoli and Lee, 2004; Onushko et al.,

**Fig. 4.** (A) Topographical plots showing the distribution of alpha TR-Power before (baseline), immediately after (post) and 24 h after (retention) motor practice. Cooler colors represent lower TR-Power, black dots represent the electrodes used to define the ROIs. (B–D) Change in TR-Power over time in the different ROIs: (B) frontal; (C) Motor; (D) Parietal. Values are presented separately for P-LD (blue), P-MD (green) and P-HD (orange). Dots in the background represent individual participants and shaded areas denote 95% confidence intervals. \*Main effect of time at  $p < 0.05$ ; †Difficulty  $\times$  time interaction at  $p < 0.05$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



2014). Although older adults practicing at high difficulty task did not report a higher mental workload on the NASA-TLX and were able to improve during the practice phase, the task was probably still too difficult to consolidate the learned skill successfully into memory (Fig. 2B).

**Practice-related decrease in alpha and beta TR-Power**

The mirror star tracing task induced activation of the whole brain, as evidenced by negative alpha and beta TR-Power during task execution in all areas. For alpha power in the motor cortex and beta power in the frontal cortex, TR-Power was lower in the ipsi-compared to the contralateral hemispheres. The right frontal and parietal cortices both play important roles in the integration of sensory and motor information, which is necessary for successful performance on the mirror star tracing task (Halsband and Lange, 2006). Contrary to previous findings in young adults (Rietschel et al., 2012; Bueteftisch et al., 2014), task difficulty did not affect TR-Power during the baseline phase. Again, this might have been due to the rapid initial learning over the baseline blocks, which increased the amount of variability in the TR-Power data.

Both alpha and beta TR-Power decreased immediately after practice, indicative of an increase in neural activity (Pfurtscheller and Lopes Da Silva, 1999). Increased neural activity over a single practice session might represent a transient stage of early plasticity related to motor learning (Bavelier et al., 2010) and fits with previous electrophysiological (Houweling et al., 2008; Veldman et al., 2018), magnetic stimulation (Berghuis et al., 2017) and imaging (Rieckmann et al., 2010) data in both younger and older adults. However, there are also studies in younger adults reporting decreases in neural activity after learning, mostly explained as reductions in cortical resources to successfully execute the task (Studer et al., 2010; Gehringer et al., 2018). During the acquisition of a serial reaction time task, alpha

TR-Power initially decreased during the skill acquisition phase until full explicit knowledge of the sequence was reached, after which TR-Power increased below baseline (Zhuang et al., 1997). These results suggest that the direction of changes in neural activity is related to the learning phase so that activity initially increases until automatization of task execution is achieved, after which a decrease in activity will be seen. Arguably, participants in the current study did not reach automatization after a single practice period. This is consistent with the lack of consolidation of movement time and the observation that alpha and beta TR-Power returned to baseline levels at 24-h retention in all areas for all difficulty groups.

### Failure to engage neural plasticity after practice at a high difficulty level

The observed decrease in alpha TR-Power in the frontal and parietal cortices during the skill acquisition phase was dependent on task difficulty. In these regions, decreased TR-Power during skill acquisition was only present after P-LD and P-MD, but not after P-HD. Decreased task-related alpha power in the frontoparietal network has been related to cognitive-motor processing, attention, and memory encoding (Klimesch, 1999; Jensen and Mazaheri, 2010). Therefore, the unchanged alpha TR-Power might indicate insufficient processing of task-related information on the group level during execution of the task at the highest difficulty. Combined, the reduced motor skill retention and failure to engage neural plasticity for participants who practiced at the highest difficulty are in line with studies reporting an age-related deterioration in learning rate and neural adaptations (King et al., 2013; Rueda-Delgado et al., 2019). These results support the hypothesis that an age-related deterioration of motor learning could be specific for motor tasks with a high difficulty level. However, a control group of young adults is necessary to confirm this hypothesis.

It should be noted that changes in TR-Power could be influenced by a practice-induced increase in resting power, explained in previous studies as a transient reduction in cortical excitability directly after motor practice to prevent interference (Ziemann et al., 2004; Espenhahn et al., 2019). In the present study, there was indeed an increase in resting power from pre to post, which was independent of difficulty level or brain area (data not shown). However, effects of task difficulty as described in the previous paragraph were not seen in resting power changes. Furthermore, it is known that different brain networks are active in the resting brain com-

pared to during task performance (Hahn et al., 2018). Therefore, this explanation is probably not relevant for the current TR-Power data.

### Behavioral and neural changes are not correlated

Although the changes in TR-Power seem to parallel changes in motor performance, these changes did not correlate with each other. As already discussed, the rapid initial learning in the baseline phase might have obscured the effects of task difficulty. Therefore, the first ten trials of practice were taken as a pre-test measure of motor performance. However, no EEG data were available during this practice block and therefore, correlation analyses were done with data from the baseline phase. Had we measured TR-Power at the beginning of practice, we might have seen relations between motor learning and neural adaptations in accordance with previous studies (Pollok et al., 2014; Veldman et al., 2018). In addition, it is also possible that other neural mechanisms, such as changes in interregional connectivity (Veldman et al., 2018; Wu et al., 2018) or cortical inhibition (Mary et al., 2015; Mirdamadi and Block, 2020) play a more prominent role in the learning of this specific task.

### Limitations

The generalizability of these results is subject to limitations. Firstly, a lack of a control group of younger adults does not allow us to make definitive statements as to how age interacts with task difficulty in motor skill acquisition and retention. In two previous studies using the same task, younger adults were able to learn and retain the skill at all difficulty levels, supporting the hypothesis that impaired learning of tasks with a high difficulty level is an age-specific phenomenon (Joseph et al., 2013; Bootsma et al., 2018). However, in both studies the practice period was longer than that employed in the current study, complicating direct comparisons. In contrast, studies employing different motor learning tasks did report impaired learning at high difficulty levels also in younger adults, especially when the self-reported mental workload was high (Akizuki and Ohashi, 2015; Shuggi et al., 2017). Thus, it could be that the impaired learning at the high difficulty found in the current study is a feature of motor learning that is independent of age. Secondly, the current results might not be generalizable to all types of motor skills. Previous studies have noted that the neural correlates of motor learning, as well as age-related

**Fig. 5.** (A) Topographical plots showing the distribution of beta TR-Power before (baseline), immediately after (post) and 24 h after (retention) motor practice. Cooler colors represent lower TR-Power, black dots represent the electrodes used to define the ROIs. (B–D) Change in TR-Power over time in the different ROIs: (B) frontal; (C) Motor; (D) Parietal. Values are presented separately for P-LD (blue), P-MD (green) and P-HD (orange). Dots in the background represent individual participants and shaded areas denote 95% confidence intervals. \*Main effect of time at  $p < 0.05$ ; †Difficulty  $\times$  time interaction at  $p < 0.05$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

declines in motor learning, are task-specific (Seidler, 2006; Hardwick et al., 2013; Berghuis et al., 2017). The task used in the current study was a continuous tracing task and the focus was on learning to adapt hand movements to changing circumstances (i.e., mirror feedback). The results might therefore not generalize to other types of skills such as learning a discrete task like reaching to a cup or a more complex motor skill like basketball dribbling. Thirdly, trial-wise baseline correction for the EEG data was not possible in the current design and therefore, TR-Power was calculated relative to a pre-task resting-state condition. As discussed above, changes in TR-Power should thus always be regarded in relation to resting-state power. Lastly, although EEG has a high temporal resolution and allows monitoring of brain activity during complex tasks, the spatial resolution is limited. In the current study, we therefore refrained from detailed localization but rather defined ROIs based on broader brain areas. Further research combining EEG with functional magnetic resonance imaging is needed to gain more insight into the specific localization of the observed effects and identify the involvement of subcortical areas potentially involved in motor learning.

In conclusion, the current study showed that not only did task difficulty affect the magnitude of motor skill learning but it did also affect the underlying neural mechanisms. Practicing a star-tracing motor skill at a high difficulty level hindered its consolidation into motor memory in healthy older adults and reduced modification of task-related alpha power after practice. Furthermore, the results emphasize the importance to monitor practice-related changes in both spatial and temporal aspects of a motor task in older adults, because age seems to affect these skill elements differently. Taken together, our findings show that a failure to engage neural plasticity through practice of a high-difficulty task is accompanied by reduced motor skill retention in older adults. These data help us better understand how older adults learn new motor skills and might have implications for prescribing motor skill practice according to its difficulty in rehabilitation settings.

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## DECLARATIONS OF INTEREST

None.

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## APPENDIX A. SUPPLEMENTARY DATA

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