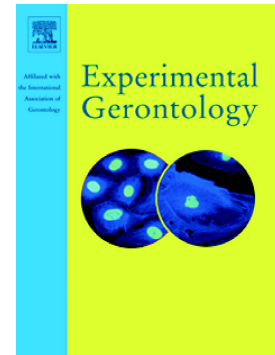


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Eva-Maria Reuter, Gregory E.P. Pearcey, Timothy J. Carroll



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## **Greater neural responses to trajectory errors are associated with superior force field adaptation in older adults**

Running Head: Error processing during force field adaptation

Eva-Maria Reuter<sup>1</sup>, Gregory E.P. Pearcey<sup>2</sup>, Timothy J. Carroll<sup>1</sup>

<sup>1</sup>Centre for Sensorimotor Performance, School of Human Movement and Nutrition Sciences;  
The University of Queensland

<sup>2</sup>Rehabilitation Neuroscience Laboratory, School of Exercise Science, Physical and Health Education;  
University of Victoria

Correspondence to this article should be directed to:

Eva-Maria Reuter, School of Human Movement and Nutrition Sciences, The University of  
Queensland, Brisbane, QLD 4072, email: e.reuter@uq.edu.au, phone: (+61 7) 3365 6104

## Abstract

Although age-related declines in cognitive, sensory and motor capacities are well documented, current evidence is mixed as to whether or not aging impairs sensorimotor adaptation to a novel dynamic environment. More importantly, the extent to which any deficits in sensorimotor adaptation are due to general impairments in neural plasticity, or impairments in the specific processes that drive adaptation is unclear. Here we investigated whether there are age-related differences in electrophysiological responses to reaching endpoint and trajectory errors caused by a novel force field, and whether markers of error processing relate to the ability of older adults to adapt their movements. Older and young adults ( $N = 24/\text{group}$ , both sexes) performed 600 reaches to visual targets, and received audio-visual feedback about task success or failure after each trial. A velocity-dependent curl field pushed the hand to one side during each reach. We extracted ERPs time-locked to movement onset [kinematic error-related negativity (kERN)], and the presentation of success/failure feedback [feedback error-related negativity (fERN)]. At a group level, older adults did not differ from young adults in the rate or extent of sensorimotor adaptation, but EEG responses to both trajectory errors and task errors were reduced in the older group. Most interestingly, the amplitude of the kERN correlated with the rate and extent of sensorimotor adaptation in older adults. Thus, older adults with an impaired capacity for encoding kinematic trajectory errors also have compromised abilities to adapt their movements in a novel dynamic environment.

*Keywords:* aging; electroencephalography (EEG); event related potential; error-related negativity; feedback-related negativity; sensorimotor adaptation

## Introduction

Sensorimotor adaptation is an error-based learning process (Izawa & Shadmehr, 2011) that is required to maintain successful and efficient movements despite changes in the properties of the environment or the body, such as during recovery after injury or disease, as well as age-related changes (King, Fogel, Albouy, & Doyon, 2013). Typical paradigms to study adaptation in the upper limbs are visuomotor rotation (Cunningham, 1989; Krakauer, 2009) and force field adaptation (Shadmehr & Mussa-Ivaldi, 1994). During visuomotor rotation, participants reach at targets while adapting to rotated visual feedback (for review see Krakauer, 2009). During force field adaptation participants hold a robotic arm and reach at visual targets, while the robot applies velocity-dependent forces orthogonally to the reach direction. This lateral perturbation initially leads to large spatial errors and curved movements, but with practice, participants reduce errors and perform accurate and straight reaching movements by modifying their force output in a velocity-dependant way (see Krakauer & Mazzoni, 2011 for review). To date the majority of studies investigating age-related differences in sensorimotor adaptation employed visuomotor rotation paradigms (e.g. Bock, 2005; Buch, Young, & Contreras-Vidal, 2003; Hegele & Heuer, 2013; Heuer & Hegele, 2008, 2014; Heuer, Hegele, & Sulzenbruck, 2011; for review see King et al., 2013; Seidler, 2006). Compared to visuomotor rotations, adaptation to physical perturbations, such as force fields, more closely resembles the requirements faced by older adults to adapt their force output in everyday life as a consequence of muscle atrophy, or injury. Force field adaptation therefore appears to be a good model to study motor adaptability in older people. However, to the best of our knowledge, only three studies to date have compared force field adaptation between young and older adults, and results are inconsistent between the studies (Cesqui, Macrì, Dario, & Micera, 2008; Huang & Ahmed, 2014; Trewartha, Garcia, Wolpert, & Flanagan, 2014). Specifically, while Cesqui et al., 2008 and Trewartha et al., 2014, found no differences in kinematic error reduction between young and older adults, Huang and Ahmed, 2014 reported that older adults reduced errors less than young adults when reaching in a force field. Errors in hand position when exposed to a force field can be influenced by both online feedback corrections and feedforward or predictive compensation for the field. However, two of these studies included

force channel trials to isolate predictive control mechanisms in adaptation. In channel trials, a straight-line path between the start and the target position is enforced with a mechanical force channel (Scheidt, Reinkensmeyer, Conditt, Rymer, & Mussa-Ivaldi, 2000). The velocity-dependent force applied against the channel wall in such “error clamp” trials indicates how well participants predict the new dynamics, independent of feedback and online corrections. Huang and Ahmed, 2014 found that younger adults showed greater predictive compensation to the field in force channel trials than older adults, suggesting a decline in the ability to form an accurate internal representation of new dynamics with increasing age. By contrast, Trewartha et al., 2014 found no age-related differences in predictive force field compensation. To resolve these opposing findings, it is important to identify whether there are changes in the mechanisms that underpin force field adaptation with age.

Accordingly, the purpose of the current study was to investigate whether processes that drive adaptation to new dynamics, such as the processing and correction of errors, differ between young and older adults. Therefore, we not only assessed behavioural performance in young and older adults adapting to force fields, but also the neural responses to errors during the adaptation task. We aimed to establish whether error processing is associated with any age-related deficits of force field adaptation.

People typically experience both sensory prediction and task outcome errors when first exposed to a novel force field (Izawa & Shadmehr, 2011). In this paradigm, sensory prediction errors (also referred to as low level errors, see Krigolson & Holroyd, 2007) constitute mismatches between the actual, laterally perturbed, reach trajectories and the straight trajectories that are expected given the issued motor commands. Task errors (also referred to as high level errors, see Krigolson & Holroyd, 2007) occur when people miss the intended target, and therefore fail to attain the task goal. Evaluation of both error types can drive the behavioural changes that take place in motor commands during adaptation (Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015; Taylor, Hieber, & Ivry, 2013). However, the processing of sensory prediction errors seems to drive the ‘true’ adaptation that reflects predictive compensation for the new dynamics (Butcher & Taylor, 2017; Izawa & Shadmehr, 2011; Shadmehr, Smith, & Krakauer, 2010). In this study, we considered responses to both of the error types

that can influence adaptive behaviour, given that little is known regarding the contribution of different errors to adaptation in older adults.

Error processing can be measured with EEG. In speeded choice response tasks, there is a negative EEG response to the commission of errors, referred to as error negativity (NE; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991) or error-related negativity (ERN; Gehring, Goss, Coles, Meyer, & Donchin, 1993), and a similar negativity to negative task feedback, referred to as feedback related negativity Miltner (fERN/FRN; Miltner, Braun, & Coles, 1997). Both ERN and fERN are reduced in older adults (e.g. Band & Kok, 2000; Falkenstein, Hoormann, & Hohnsbein, 2001; Nieuwenhuis et al., 2002), suggesting a reduced sensitivity to errors with age.

In sum, our goal was to investigate age-related differences in force field adaptation and to gain a better understanding towards why some older adults seem to adapt less than young adults, while others do not seem to differ with regard to their adaptation outcomes. We expected that the ability to process sensory prediction errors and task errors might be a key determinant for adaptability in the elderly. More precisely, we addressed three aims in the current study. First, we compared how groups of older and young adults adapted to novel dynamics. Specifically, we characterised older adult's behaviour in force field adaptation by describing movement parameters (movement time, velocity, extend, smoothness), and by measuring error-reduction during exposure to the force field and predictive compensation in channel trials (i.e. 'true' feedforward adaptation). We predicted that young and older adults would adapt to the new dynamics (Cesqui et al., 2008; Huang & Ahmed, 2014; Trewartha et al., 2014), but expected reduced adaptation in seniors, consistent with reports of motor and cognitive functional decline with age (for reviews see e.g. King et al., 2013; Maes, Gooijers, de Xivry, Swinnen, & Boisgontier, 2017; Park & Festini, 2017). Second, we evaluated whether there were age-related differences in electrophysiological responses to sensory prediction errors (trajectory errors during reaching) and task errors experienced during adaptation. Following Torrecillos et al., (2014) we used EEG to measure error processing during sensorimotor adaptation (Sambrook & Goslin, 2015; Torrecillos et al., 2014). Based on previous findings on error processing in the elderly employing task with a simple motor response (e.g. Falkenstein et al., 2001; Nieuwenhuis et al., 2002),

we expected that ERP amplitudes associated with the commission of errors and the evaluation of task outcome feedback would be reduced for older adults. Third, we tested the hypothesis that markers of error processing would be associated with adaptation outcomes in both young and older adults. In particular, as adaptation is an error-based learning process, we expected that older adults, who have a larger (more youth-like) brain response to errors, are more capable of adaptation.

We found that older adults did not differ on average from young adults in the rate or extent of sensorimotor adaptation. However, responses to both trajectory errors and task errors were reduced in the older group. Interestingly, the rate and extent of adaptation were significantly larger in a subgroup of older adults with larger neural response to trajectory errors, compared to other older adults. This suggests that older adults with impaired capacity for trajectory error processing also have impaired capacity to adapt their movements to a novel dynamic environment.

## Methods

### Participants

Twenty-eight young (17 to 24 years of age) and 26 older (65 to 80 years of age) healthy participants were recruited from the student pool from The University of Queensland and the community, respectively. All participants gave written informed consent to take part in the study and received either credit points or AUD 20 for their participation. They reported to be right handed (Oldfield 1971, as modified by M. Cohen, Staglin IMHRO Center for Cognitive Neuroscience, University of California, Los Angeles, Los Angeles, CA; <http://www.brainmapping.org/shared/Edinburgh.php>), to have normal or corrected to normal vision and hearing, and to be free of any neurological or psychiatric disorders. Moreover, we asked participants to self-report their health (3 items), and years of education. Older participants additionally underwent the Standardised Mini-Mental State Examination (SMMSE; Molloy, Alemayehu, & Roberts, 1991) to ensure that they did not suffer from cognitive impairment and hence were able to understand and follow the task instructions. All older participants scored higher than 26 points on the SMMSE, indicating normal function. The Human

Research Ethics Committee of the University of Queensland, Australia, approved the study (Approval Number 2015000781).

One older and three young participants were excluded as they hit the targets in less than 12% of the trials, resulting in less than the 50 valid trials required for EEG analysis time-locked to the successful target hit (Marco-Pallares, Cucurell, Münte, Strien, & Rodriguez-Fornells, 2011). One older additional participant had to be excluded due to noisy EEG signals. The final sample consisted of 25 young (15 females, mean age of  $19.04 \pm 2.0$  years) and 24 older participants (8 females, mean age of  $69.67 \pm 4.3$  years). Final samples did not differ with regard to their subjective rating of health (young:  $2.64 \pm 0.78$ ; older:  $2.26 \pm 0.79$ ; a higher score indicates better health rating), or handedness (young:  $0.79 \pm 0.14$ ; older:  $0.77 \pm 0.24$ ; ranging from -1 indicating left handedness to +1 for right handedness). Older adults, however experienced more ( $F(1,47) = 20.247, p < .001$ ) years of education ( $18.1 \pm 5.2$  years) than the younger adults ( $13.2 \pm 1.5$  years), which is likely because we recruited young adults from a first year student pool and older adults from the broader university community. Due to an EEG trigger failure, we had to exclude one additional older participant from the analysis of trajectory error processing (task error was triggered using a photo sensor, hence data from this person were included in the behavioural and task error analyses only).

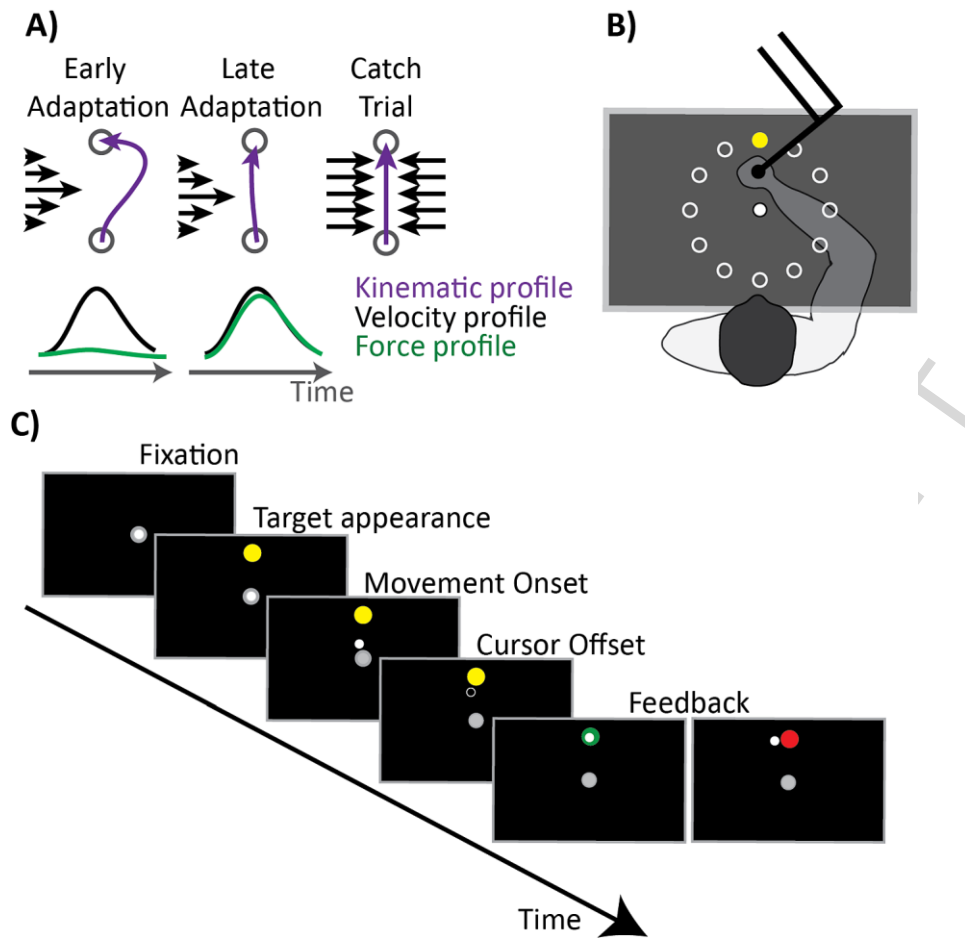
### **Reaching Task and Procedure**

Participants made planar reaches with their right arm while grasping the handle of a robotic arm; the vBOT, which is a modular, two-dimensional planar manipulandum (see Figure 1; for full detail of the apparatus see Howard, Ingram, & Wolpert, 2009). Visual feedback was provided using a 27" LCD computer monitor (ASUS, VG278H) running at 120Hz mounted above the vBOT and projected to the participant via a mirror. The display was calibrated so that visual feedback appeared in the plane of the limb, and a cursor appearance veridically coincided with actual hand position. The mirror prevented vision of the manipulandum and the participant's arm. The participant's arm rested on an air-sled that allowed for near frictionless movement over the table while relaxing their shoulder muscles.



The participants' task was to move a cursor (radius = 0.25 cm), representing the position of their hand, from a start position (white disc with 1 cm radius, positioned on the mid-sagittal plane ~25 cm from the participant's chest, and ~23 cm from the centre of the eyes) to a target position (yellow disc with 1 cm radius positioned 10 cm away from the start position) by making a reaching movement after a go signal. Targets could appear in one of twelve positions, distributed evenly in 30-degree increments around the start position. Target order was pseudorandomised, such that each target was presented once within each block of twelve trials.

Participants were instructed to make a single, smooth and swift movement from the start to the target position in an attempt to stop on the target (see Figure 1C for a schematic overview of the trial structure). Once they stopped their movement (speed < 0.5 cm/s) they immediately received bimodal audio-visual feedback on their success. When the participant hit, or sliced through the target, the target disc turned green, and a pleasant "bing" sound was played. When they missed it (i.e. stopped short, or reached the target extent on either side of the target), the target disc turned red and an alternative sound was played. The start and the target position were displayed throughout the whole trial but the cursor feedback was displayed only until the reach extended 5 cm away from the start position (i.e. during the first half of the reach), as we aimed to minimise predictive processing of task outcome (based on vision) prior to the end of the reaching movement. The cursor position was displayed again at the end of each trial, together with the presentation of the audio-visual task feedback. If the participant's reach exceeded the target distance, the cursor was displayed at the point where they passed a 10 cm radius. Feedback was provided for 800 ms, and participants were instructed to stay and wait in their final position until the feedback was turned off before returning back to the start position. When a participant's movement time was below 150 ms or greater than 450 ms, an additional feedback message was presented, asking them to move slower or faster, respectively. Importantly, this additional feedback message was presented after the task feedback, and was provided in order to ensure that participants moved with approximately the same movement speed. No feedback about speed was provided when participants' movement time was within the desired range.



*Figure 1:* A) Schematic illustration of force field adaptation. In early adaptation kinematic profiles are curved, and participants do not produce velocity dependent forces to counteract the force field. In late adaptation, kinematics are straight and temporal profiles of the lateral hand forces exerted to counteract the forces produced by the robot match the hand speed profiles. In force channel catch trials, a stiff two-dimensional spring constrains reaches to follow a straight path to the target, and predictive hand forces made to counteract the expected perturbation are measured. B) Experimental set up. Participants held the v-Bot arm handle and performed centre-out reaching movements to targets presented at one of twelve positions (note that opacity of the screen and open circles at each target position are for illustration purposes only). C) Task structure. After a central fixation, a target appeared and participants initiated their reach towards the target. Mid-reach the cursor disappeared. At the end of each trial (either when the participant stopped, or when the target extent was reached), feedback was given to the participant about whether they hit or missed the target and the location of the cursor at target extent.

This reaching task was performed in three different dynamic environments that were generated by the robot: 1) a null field in which the robot imposed no forces, 2) a viscous curl field imposing forces of  $25 \text{ N}\cdot\text{m}^{-1}\cdot\text{s}$ , and 3) a force channel that constrained reaches to follow a straight path to the target with a

spring constant of 4,000 N/m orthogonal to the channel wall (see also Carroll, de Ruyg, Howard, Ingram, & Wolpert, 2016; Reuter, Cunnington, Mattingley, Riek, & Carroll, 2016). The force field and channels were only imposed on the outward movements towards the targets, whereas a weak spring assisted the participants to return the handle to the start position. No feedback about the hand position was provided during the return movement to avoid unlearning.

Participants performed 600 reaches in total, of which the first 96 were baseline trials (80 null field trials with no forces, and 16 channel trials), and 504 were adaptation trials (420 force field trials, and 84 channel trials). The direction of the force field was counterbalanced between participants. The order of field trials and channel trials was pseudorandomized for each participant, so that there was one channel trial and five field trials within six consecutive trials. Participants were forced to take a 45 s break after each block of 60 trials, and told that they could take additional breaks anytime, by releasing the handle, and thus pausing the experiment. The reaching experiment took approximately 50 minutes, preceded by a familiarisation phase, and EEG set up. In the familiarisation phase, participants performed movements in the null field until they felt comfortable doing the task and were able to move within the speed constraints. Participants performed at least 60 familiarisation trials in three blocks of 20 each. In the first block, we wanted participants to get familiar with the device and the task. Participants could move at their preferred speed. In the second block, participants received feedback about their movement speed if they moved too slow or too fast. In order to facilitate the adjustment of reaching speed to the task requirements only a single target position (at 90 degrees) was presented. The third practice block was identical to the experimental baseline trials with targets at all 12 positions. If a participant struggled with any of the training blocks, or indicated that he/she would prefer more practice, the training block was repeated. The position of the handle and perpendicular forces were recorded with a 1000 Hz sampling rate.

### **Behavioural data analysis**

Behavioural data were analysed with MATLAB 2015a (MathWorks Inc.). A 5th order, Butterworth filter with a low-pass cut-off frequency of 50Hz was applied to position, force and velocity data prior to analysis. The movement initiation was measured through the application of Teasdale's et al. (1993)

algorithm to the velocity profile for each movement, with an initial threshold of 10% of the maximum tangential speed. Movement time was calculated from movement initiation until the participants reached the target distance of 10 cm, or reduced its velocity to more than 0.5 cm/s, if target distance was not reached. Trials where participants did not reach a distance of 5 cm, i.e. less than half of the target distance, were excluded from all further behavioural and EEG data analysis. On average  $5.8 \pm 1.09$  trials in the young group and  $4.25 \pm 0.87$  trials in the older group were excluded, which is less than 1% of all trials per person. We analysed the percentage of target hits, the maximal reach distance, the peak velocity, the reach distance at peak velocity, and the movement time to generally describe participant's behaviour in the task at baseline and during adaptation. In order to characterise kinematic reaching errors at baseline, we analysed peak perpendicular error, signed peak perpendicular error in the direction of the upcoming force field, and curvature of the movement (path length from start to final position/distance from start to final position) averaged across all of the null field trials during the baseline period. For field trials in the adaptation phase we analysed curvature and the signed peak perpendicular error in the direction of the force field. Variables for the adaptation phase were averaged across consecutive field trials in bins of 12, such that 35 bins characterised the entire adaption period.

For channel trials, which were intermittent in the baseline and the adaptation phases, we calculated the signed peak force applied to counteract the force of the robot in order to characterise predictive compensation for the new dynamics. Signed peak forces were averaged across the entire baseline period, and across 3 consecutive channel trials in the adaptation phase.

### **EEG recording and analysis**

EEG data were recorded using a 64 channel active electrode system (actiCHamp, Brain Products, Munich, Germany). Electrodes were positioned according to the extended 10-20 system (Jasper, 1958). The signal was acquired with a sampling rate of 2500 Hz and low pass filtered at 100 Hz. Offline analyses of the EEG data were performed using Brain Vision Analyzer Software 2.0 (Brain Products, Munich, Germany). For ERP analyses, the signal was offline down-sampled to 625 Hz and

re-reference to the grand average signal (average across all 64 channels). A high-pass filter of 0.1 Hz, a low-pass filter of 30 Hz and a notch filter of 50 Hz were applied.

Following Torrecillos' et al. (2014), we measured processing of trajectory and task errors as error-related negativities in the event-related EEG potential. Specifically, we quantified kinematic trajectory error processing based on EEG activity time-locked to the movement onset. Task error processing was quantified based on EEG activity time-locked to feedback onset. For kinematic and trajectory error analysis, the data were segmented in 1 s segments of -200 to 800 ms from movement onset or feedback onset and baseline corrected relative to the 200 ms period prior to movement or feedback onset, respectively. Note that due to movement related potentials preceding movement onset (Jahanshahi & Hallett, 2003), and ongoing motor processing during movement prior to feedback onset, baseline phases prior to our ERP segments are not flat. Eye movements were corrected using ocular artefact removal based on an established algorithm (Gratton, Coles, & Donchin, 1983). EEG activity with a gradient steeper than  $5 \mu\text{V}/\text{ms}$ , voltages exceeding  $-100 \mu\text{V}$  or  $100 \mu\text{V}$ , or voltage changes of more than  $100 \mu\text{V}$  in a 100ms time window were automatically detected and rejected as artefacts. Trials with artefacts were excluded channel-wise from further analysis (i.e. segments with artefacts were only excluded for channels in which the artefact occurred). Both kinematic and task error processing was analysed at electrode position FCz, which is situated over the medial–frontal cortex and which is a standard electrode site for analysis of error-related EEG potentials (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Krigolson, 2017).

For task error processing, following the traditional difference wave approach for feedback error related negativity (fERN) analysis (for reviews on fERN (also FRN) see e.g. Krigolson, 2017; San Martín, 2012), we calculated difference waves between trials with positive and negative feedback. The fERN peak was defined as the maximum negative peak in this fERN difference wave signal ( $\Delta\text{fERN}$ ) between 150 and 350 ms after feedback onset and peak latencies and adaptive mean amplitudes ( $\pm 20\text{ms}$ ) were extracted. Additionally we analyzed a feedback-related positivity ( $\Delta\text{fPE}$ ), which was evident in difference waves and peaked at about 400 ms (see Figure 5). Again, following Torrecillos et al. (2014), we further analysed kinematic trajectory error processing by comparing

mean ERP amplitudes gained from quartiles of trials with different error sizes (determined as the maximal perpendicular error per trial, i.e. the deviation from a straight trajectory from start to target position). Quartiles were determined individually for each participant, to allow for an equal number of trials in each error size category. We calculated kinematic error-related negativity (kERN) difference waves by subtracting the mean ERP amplitudes gained from the quartile of trials in which the smallest trajectory errors occurred from the mean ERP amplitudes gained from the quartile of trials in which the largest trajectory errors occurred. A more negative signal in this difference wave represents larger kinematic error processing. In young adults, a clear negative peak around 180 ms after movement onset was evident in the difference wave (see Figure 6c). We refer to this peak in the difference wave as kinematic error-related negativity ( $\Delta$ kERN), inspired by Torrecillos et al., 2014, who used the term ERN-k. Note that the  $\Delta$ kERN latencies in our complex reaching task are later than those typically reported for ERNs in speeded choice response tasks (Nieuwenhuis, Holroyd, Mol, & Coles, 2004), in which errors are binary in nature (Anguera, Seidler, & Gehring, 2009). This makes sense, as sensory prediction errors during reaching in a force field cannot readily be evaluated by use of the efference copy signal alone [as it would be the case in classic ERN speeded choice response paradigms or discrete motor task (Holroyd & Coles, 2002; Joch, Hegele, Maurer, Müller, & Maurer, 2017; Krigolson, 2017)]; instead in our task visual and/or proprioceptive feedback about the position of the hand are required to evaluate the discrepancy between the expected and actual sensory consequences (Torrecillos et al., 2014). Consequently, the kERN might more closely resemble an fERN than a classic ERN (Torrecillos et al., 2014). We quantified this  $\Delta$ kERN peak in each subject by extracting the peak latencies and adaptive mean amplitudes ( $\pm 20$  ms) of peaks detected between 120 and 250 ms in the difference wave signal. In addition, we also exported average amplitudes for all four quartiles from a 50 ms time window of 160 – 210 ms after movement onset in order to test for scaling of kinematic error processing ERPs with error size.

### Statistical analysis

Statistical analyses were done with SPSS for Windows version 25.0 (IBM Corp., Armonk, NY) and MATLAB 2015a (MathWorks Inc.). Behavioural measures at baseline were analysed with univariate

ANOVAs with the between group factor AGE (young, older). Mixed design ANOVAs and ANCOVAs were employed for the adaptation phase with the factors AGE and BIN (1 to 35) for dependent variables measured in field trials, and AGE and Bin (1 to 28) for signed peak forces measured the channel trials. ANCOVAs were used if we found any baseline differences between groups in the respective measure and baseline, and if this was the case the baseline value for the respective variables were included as a covariate in the model. Significant interactions between the factors BIN and AGE were followed up by determining learning rate constants from fitting the following exponential function using the Matlab *fit* function to the learning curves separately for both age groups:

$$y = ae^{-bx} + c$$

where  $x$  = trial number,  $a$  = a constant to allow for baseline error,  $b$  = the learning rate constant,  $y$  = reach error, and  $c$  = the asymptotic reach error. Confidence intervals (95%) for the learning rate constants were obtained by fitting to mean errors from bootstrapped samples (10000 iterations with replacement).

For ERP analysis we calculated ANOVAs with the factors ERROR SIZE (quartile 1 to 4) on ERPs time locked to movement onset to assess whether kinematic error processing scales with error size. We further employed one sample t-test on the  $\Delta$ kERN,  $\Delta$ fERN, and  $\Delta$ fEP difference wave peak amplitudes separately for both age groups. Between group differences in error processing were investigated with univariate ANOVAs on adaptive mean amplitudes and peak latencies. All statistical tests were computed bidirectionally. For within-subject factors, the Huynh–Feldt non-sphericity correction was applied where appropriate. Effect sizes are given as partial eta squares ( $\eta_p^2$ ).

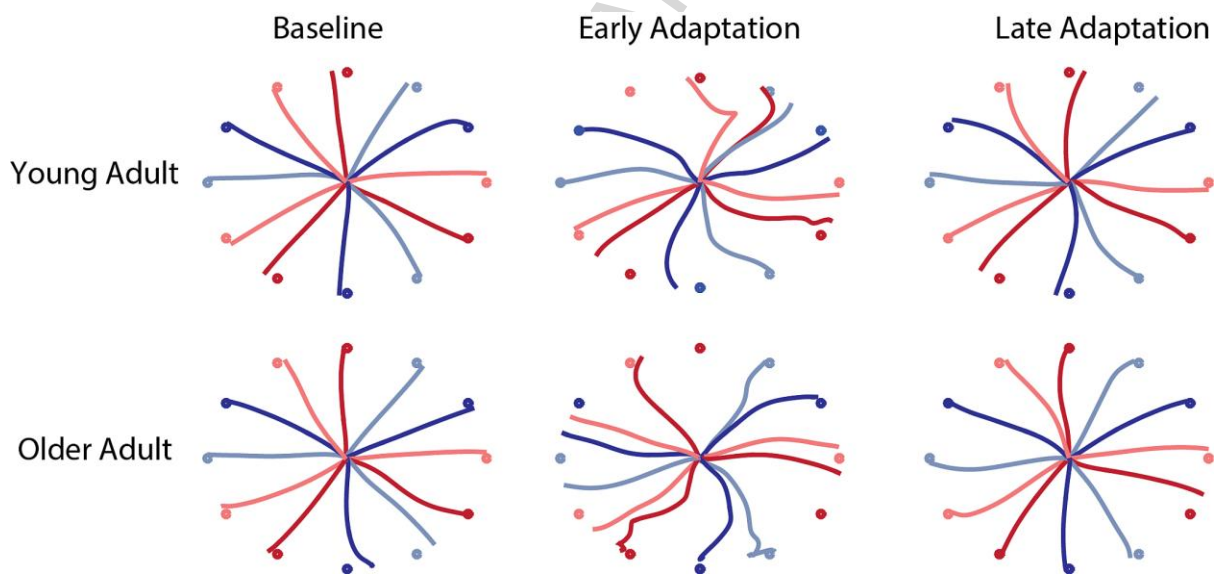
Correlations were used to investigate interrelations between the final level of adaptation and error processing ( $\Delta$ kERN amplitude,  $\Delta$ fERN amplitude). The final level of adaptation was defined as mean signed peak force averaged across second half of channel trials (i.e. bins 15 to 28), where performance reached an asymptote level (see Figure 4F). Specifically, robust Spearman skipped correlations were

computed using an open source toolbox for robust correlation analysis (Pernet, Wilcox, & Rousselet, 2013; Rousselet & Pernet, 2012). The toolbox uses Bonferroni correction for multiple comparison corrections and adjusts confidence intervals for correlation coefficients to 97.5% accordingly. Additionally, we performed median split analyses and subdivided the groups of young and older adults based on their  $\Delta$ kERN amplitudes. We then compared behaviour performance between subgroups, as outlined above for the comparison between age groups.

## Results

### Aim 1: Age-related differences in force field adaptation - Behavioural results

Figures 2 and 3 depict reach trajectories and force profiles for two individual participants at baseline, and in early and late adaptation. Figure 4 shows group average performance at baseline and during the adaptation phase for both age groups.



*Figure 2:* Examples of reach trajectories for two individual participants (young, upper row; older, lower row) reaching at baseline (last baseline trial for each direction), in the beginning of adaptation (first adaptation trial for each direction), and at the end of adaptation (last adaptation trial for each direction). Note that the young participant adapts to a rightward force field and the old participant to a leftward force field.



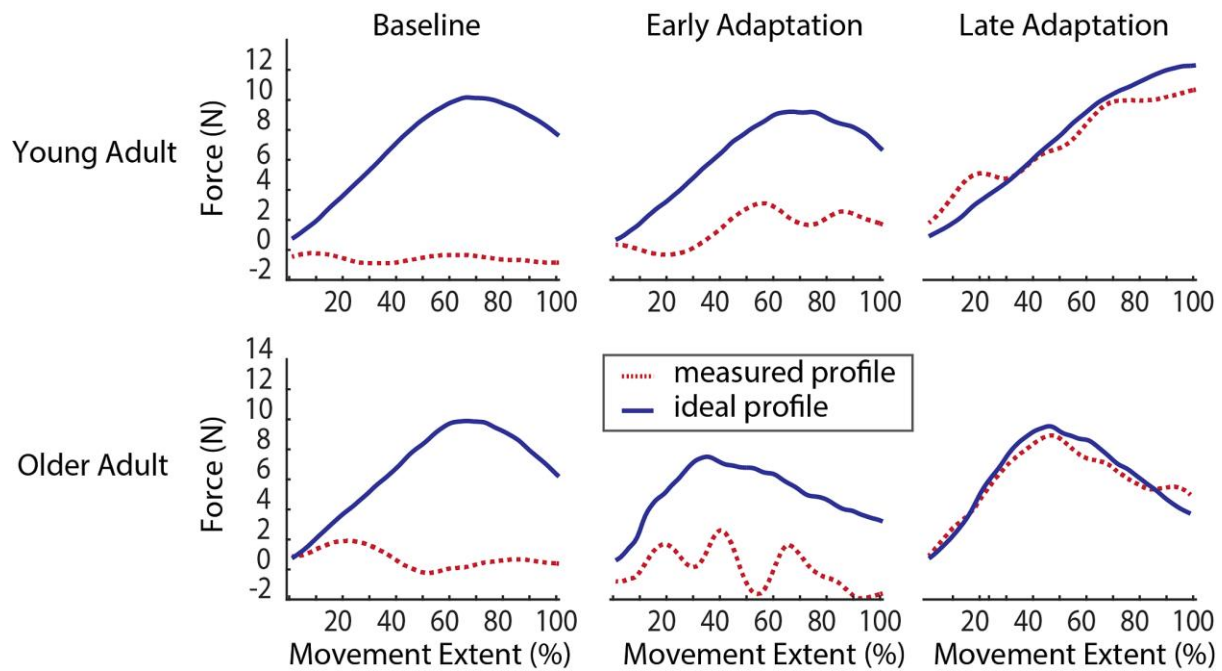


Figure 3: Examples of measured force profiles in the direction perpendicular to the direction of hand motion (red dotted line) and ideal force profiles needed to perfectly cancel the perturbing force generated by the robot (blue, solid line) for two individual participants (young, upper row; older, lower row). Individual trials recorded at the end of the baseline phase, in the beginning of adaptation, and at the end of adaptation are shown. Note that ideal force profiles also reflect the temporal course of velocity as ideal profiles are velocity dependent. Further note that ideal force profiles at baseline represent the forces that would be required to cancel the robot force when force field was subsequently turned on, and are included to illustrate that there were no substantial biases in lateral force production prior to adaptation.

*Baseline reaches in null field.* The percentage of target hits at baseline was about 75% in both groups, and despite the disappearance of the cursor midway through the reach, peak errors and movement curvature were small (Figure 4A-C). This suggests that participants made straight and smooth movements to the target, as instructed. As participants had no visual feedback of the cursor at the end of their movement, they typically reached past the target by about 2-3 cm. This overshooting was more apparent in young than older adults, evidenced by significant age effects for final reach distance and reach distance at peak velocity (see Table 1 for details). Moreover, movements of older adults were less straight, as evidenced by significantly larger movement curvature (Figure 4A), and larger lateral forces in force channel trials at baseline (Figure 4F). Peak errors in the direction of the upcoming force field, however, did not differ between age groups (Figure 4B), suggesting that there

were no age-related pre-existing direction dependent biases in reach trajectories. Also, movement time (Figure 4D) and peak velocity (Figure 4E) at baseline did not differ significantly between groups of young and older adults (see Table 1 for descriptive and statistical results for the baseline phase).

Together, these findings confirm the expected and well-described age-related reduction of smoothness with age (for reviews see Diermayr, McIsaac, & Gordon, 2011; Seidler et al., 2010), but also show that participants in both age groups were able to successfully perform the task.

Table 1. Performance measures at baseline and statistical results for comparison between age groups.

Measure	Young		Older		Statistics			
	Mean	SD	Mean	SD	F	df	p	$\eta_p^2$
Target hits (%)	76	8	74	8	0.684	1,47	.412	.014
Curvature	1.01	0.01	1.02	0.2	12.132	1,47	<b>.001</b>	.205
Signed Peak Error (cm)	0.38	0.09	0.40	0.15	0.541	1,47	.466	.011
Movement Time (ms)	323.1	66.0	350.1	44.2	2.820	1,47	.100	.057
Peak Velocity (m/s)	50.8	10.1	50.5	6.9	0.025	1,47	.876	.001
Signed Peak Force (N)	2.16	0.92	3.49	1.30	17.228	1,47	<b>.001</b>	.262
Distance at peak velocity (cm)	6.15	0.70	5.49	0.545	13.487	1,47	<b>.001</b>	.268
Reach distance (cm)	13.03	1.53	11.65	0.64	16.660	1,47	<b>.001</b>	.247

Note that target hit curvature is unitless.

*Adaptation Phase.* In the beginning of the adaptation phase, participants of both groups initially performed curved movements with large signed perpendicular errors, and lower percentage of target hits. Later in adaptation, they reduced their errors and moved straight towards the target again (see Figures 2 and 4A-C). Performance improvement is evident in all performance measures (main effects of bin for signed peak error:  $F(34,1598) = 83.926$ ,  $p < .001$ ,  $\eta_p^2 = .641$ ; curvature:  $F(34, 1564) = 24.421$ ,  $p < .001$ ,  $\eta_p^2 = .347$  (for ANCOVA model with curvature at baseline included as covariate); percentage of target hits:  $F(34,1598) = 11.992$ ,  $p < .001$ ,  $\eta_p^2 = .203$ ). With increasing task performance, the movement time was also reduced (Figure 4D; main effect of bin for movement time:  $F(34,1598) = 5.376$ ,  $p < .001$ ,  $\eta_p^2 = .103$ ).

Overall, the age groups did not differ with regard to any of the parameters characterising kinematic error (main effects of age for signed peak error, curvature, percentage of target hits, all  $p > .10$ ), but older adults had longer movement times (main effects of age for movement time:  $F(1,47) = 17.309$ ,  $p < .001$ ,  $\eta_p^2 = .269$ ). More importantly, interaction effects of the factors age and bin suggest that performance changed differently over time (Age  $\times$  Bin interactions for signed peak error:  $F(34,1598) = 2.990$ ,  $p = .004$ ,  $\eta_p^2 = .060$ ; curvature:  $F(34,1564) = 2.492$ ,  $p = .005$ ,  $\eta_p^2 = .051$  (ANCOVA model with curvature at baseline included as covariate); percentage of target hits  $F(34,1598) = 1.549$ ,  $p = .045$ ,  $\eta_p^2 = .032$ ; see Figure 4A-C). Descriptively, it seems that young adults had larger errors at the beginning of adaptation, but then reduced their errors to a greater extent than older adults and thus outperformed the older participants at the end of adaption (see Figure 4A,B). Post hoc comparisons between groups at different time points, however, did not confirm statistically significant differences between groups in either early or late adaptation. We further followed up on these interactions by analysing differences in rate constants between groups. However, error reduction rates between age groups do not suggest differences between groups (means and 95% confidence intervals from bootstrapped error reduction rate for young: mean = 0.155 [CIs: 0.106, 0.191] and older: mean = 0.220 [CIs: 0.122, 0.289] participants; curvature reduction rate for young mean = 0.229 [CIs: 0.048, 0.316] and older: mean = 0.154 [CIs: -0.001, 0.220] participants; target hit rate for young: mean = 0.069 [0.001, 0.113] and older: mean = 0.2312 [-0.350, 0.461] participants). Also, movement time changes over time differed between age group (Age  $\times$  Bin interactions for movement time:  $F(34,1598) = 1.984$ ,  $p = .032$ ,  $\eta_p^2 = .040$ ), indicating that older adults moved slower than young adults in the beginning of adaptation and then increased their movement speed over time, so that the differences in movement speed between age groups was reduced at the end of adaptation. Moreover, as in the baseline phase, velocity profiles of young and older adults were different, with young adults reaching their peak velocity later in the reach and overshooting the target distance more. We wanted participants to move as naturally as possible at their preferred movement speed and therefore did not further constrain movement times or distance. Consequently, the temporal characteristics of the force profiles experienced by the participants were slightly different for young and older adults. Most crucially however, peak velocity did not differ between age groups. Thus, the peak strength of the

physical perturbation was comparable between age groups, which allows us to investigate signed peak forces applied to compensate for the forces of the robot as a measure of feedforward adaptation. Signed peak forces increased over time in both older and younger adults (ANCOVA model with signed peak forces at baseline included as covariate, main effect of bin:  $F(27, 1242) = 3.827$ ,  $p < .001$ ,  $\eta_p^2 = .077$ ). Moreover, a Bin  $\times$  Age interaction indicates that the development of signed peak forces across adaptation differed between age groups ( $F(27, 1242) = 1.867$ ,  $p = .007$ ,  $\eta_p^2 = .039$ , see Figure 4F). A follow-up analysis on the rate of peak force development, however, did not confirm differences between groups (means and 95% confidence intervals from bootstrapped rates of peak force development for young = 0.235 [CIs: 0.114, 0.307] and older = 0.297 [CIs: 0.138, 0.446] participants).

Overall, the combined behavioural results suggest that young and older adults can adapt similarly to new dynamics even if the task is demanding (i.e. a strong force field of  $25 \text{ N m}^{-1} \text{ s}$ , discontinuous visual feedback, and twelve target positions). Both age groups reduced their kinematic errors, increased their percentage of target hits, and learned to apply predictive compensation for the new dynamics. While bin by age interactions suggest differences in the temporal characteristics of error reduction and predictive field compensation, we could not confirm any age differences in adaptation rates. We note however that performance appeared more variable between individuals in the group of older adults (i.e. larger SD, see Figure 4; and large confidence interval ranges for adaptation rates).

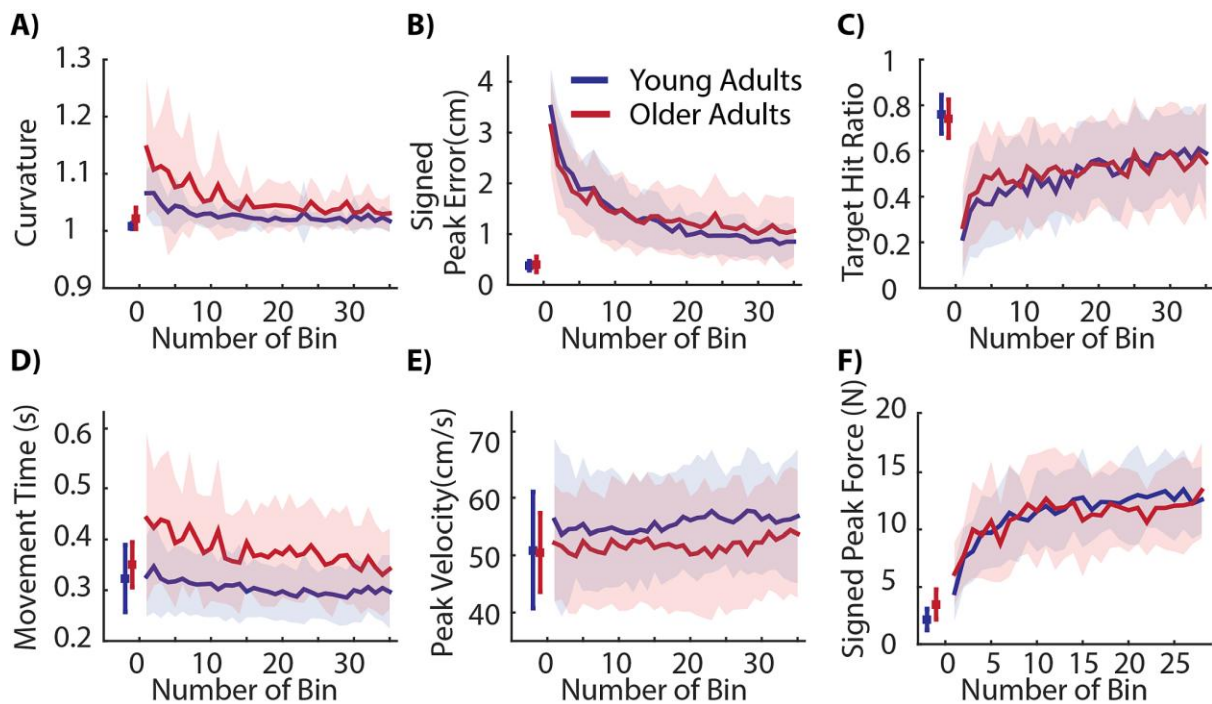


Figure 4. Behavioural performance at baseline (individual data points), and throughout the adaptation phase for young (blue) and older (red) adults. A) Curvature. B) Signed peak error at peak hand speed. C) Target Hit Ratio. D) Movement Time. E) Peak Velocity. F) Signed Peak Force. Shaded area and error bars represent standard deviations

## Aim 2: Age-related differences in electrophysiological responses to errors experienced during adaptation – EEG results

Figure 5 displays ERPs time locked to the onset of the feedback, and Figure 6 displays ERPs time-locked to the onset of the movement. We quantified trajectory error and task error processing as error-related negativities to either kinematic trajectory errors (kERN), or task errors (fERN).

### Task error processing

For task error processing, we calculated difference waves time-locked to the presentation of success/failure feedback between trials with positive feedback (target hits) and trials with negative feedback (target misses). In both groups, the difference wave showed a negative peak at approximately 200 ms, which we interpret as a  $\Delta$ fERN, and a positive peak at approximately 350ms, which we term as a  $\Delta$ fPE (see Figure 5). When outcomes can be anticipated prior to receiving task feedback, fERNs are smaller than when task feedback is unpredictable (Walsh & Anderson, 2012).

We tried to reduce this effect by turning off visual feedback at half the distance to the target, but participants still might have been able to use proprioceptive feedback to estimate their hand position in relation to the target position. Such anticipatory encoding of a target hit or miss could be responsible for the relatively early latencies of our fERN, relative to latencies reported in the literature (Hauser et al., 2014). A similar effect has been recently reported for outcome error encoding in prism adaptation (MacLean, Hassall, Ishigami, Krigolson, & Eskes, 2015). Additionally, as participants were moving their hand immediately before the feedback was presented, processes associated with movement offset and anticipation of future movement to return to the start position might have contaminated the ERP in the time period of feedback encoding. Importantly, such effects should be present independent of the feedback valence and therefore become negligible when quantifying fERNs with a difference wave approach (Eppinger, Kray, Mock, & Mecklinger, 2008; Krigolson, 2017; Nieuwenhuis et al., 2002; Torrecillos et al., 2014).

Amplitudes of both peaks in the difference wave were significantly different from zero for both young ( $\Delta fERN: t(24) = -7.305, p < .001, \Delta fPE t(24) = 4.118, p < .001$ ) and older adults ( $t(23) = -2.599, p = .016, \Delta fPE t(23) = 2.797, p = .010$ ) indicating differences in the neural response to successful and unsuccessful task outcomes, in line with earlier findings in choice response tasks (San Martín, 2012). This reliable negativity in the  $\Delta fERN$  after feedback onset indicates that both age groups successfully encoded task feedback about their final position during force field adaptation. However, the  $\Delta fERNs$  of older adults ( $-0.664 \pm SD 1.25 \mu V$ ) were significantly smaller than those of young adults ( $-3.15 \pm SD 2.16 \mu V$ ; main effect of age:  $F(1,47) = 24.114, p < .001, \eta_p^2 = .339$ ), which indicates that older adults have a reduced EEG response to negative feedback about task outcome in a reaching task.  $\Delta fERN$  latencies did not differ between age groups, nor were there differences in  $\Delta fPE$  amplitudes or latencies.

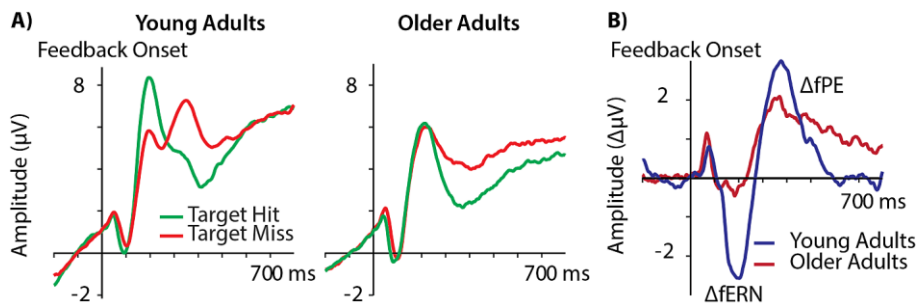


Figure 5. Event-related EEG activity, associated with task feedback processing A) Grand-average event-related potentials time-locked to task feedback onset averaged across trials with target hits (green) and target misses (red) for young (left) and older (right) adults. B) fERN differences waves (hits – misses) time locked to task feedback onset for young (blue) and red (older adults).

### Trajectory error processing

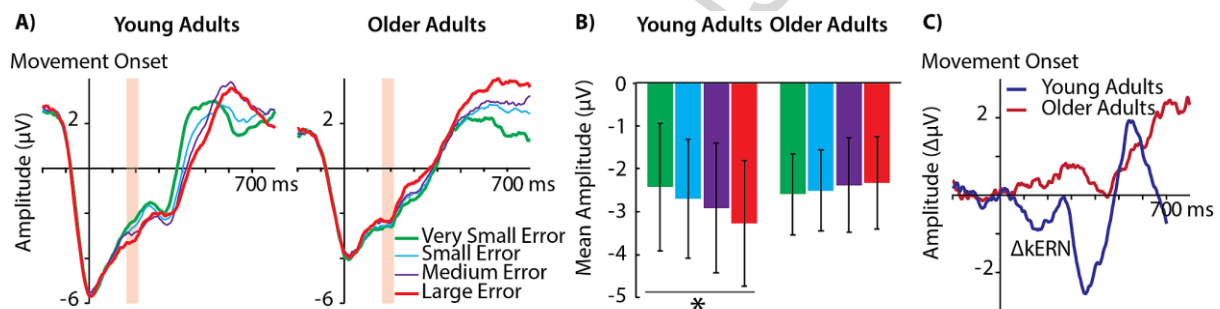
Following Torrecillos et al., (2014) we also analysed the EEG time-locked to movement onset to investigate online trajectory error processing. Trials were sorted into quartiles according to the observed perpendicular displacement in each participant and classified as: Very Small Error, Small Error, Medium Error, and Large Error trials (Torrecillos et al., 2014). Table 2 summarises the upper and lower bounds, as well as mean error size for each category and age group. Trajectory error sizes in each category were comparable between young and older adults.

Table 2. Mean Error bounds and mean error size in cm and SD for trial categories used for kERN analysis for groups of young and older adults

Groups	Very Small Error			Small Error			Medium Error			Large Error		
	Lower Bound	Upper Bound	Mean	Lower Bound	Upper Bound	Mean	Lower Bound	Upper Bound	Mean	Lower Bound	Upper Bound	Mean
Young Adults	0.14 (0.05)	0.74 (0.14)	0.49 (0.09)	0.74 (0.14)	1.26 (0.28)	0.98 (0.20)	1.26 (0.28)	2.01 (0.47)	1.60 (0.37)	2.02 (0.47)	7.34 (1.52)	3.08 (0.62)
Older adults	0.14 (0.07)	0.86 (0.32)	0.58 (0.20)	0.87 (0.32)	1.38 (0.52)	1.12 (0.42)	1.39 (0.53)	2.08 (0.74)	1.71 (0.63)	2.09 (0.74)	6.28 (1.15)	2.92 (0.87)

Note. Errors are average peak perpendicular errors in cm per group. Standard deviation is presented in brackets.

Similar to Torrecillos and colleagues' findings, grand-averaged ERP data for young adults revealed a fronto-central negativity, which increased with error size (see Figure 6 a,b). This kERN was measured at electrode FCz. Visual inspection of grand average ERPs revealed that amplitudes began to diverge approximately 130 ms after movement onset and that differences between small and larger error trials was largest between 160 and 210 ms (note that later differences between trial classes are likely to result from task feedback processing, and therefore were not regarded in the current analysis, see above for ERPs time-locked to feedback presentation). Mean activity from 160 – 210 ms after movement was more negative when trajectory errors were larger in young adults (within-subject repeated measures ANOVA with the factor error size,  $F(3, 69) = 4.062$ ,  $p = .011$ ,  $\eta^2 = .145$ ), confirming previous results from Torrecillos et al. (2014) and Anguera et al (2009).



*Figure 6.* Event-related EEG activity, associated with kinematic trajectory error processing. A) Grand-average event-related potentials time-locked to movement onset averaged across trials with very small (green) to very large (red) perpendicular errors for young (left) and older (right) adults. Difference waves were calculated between very small errors and large errors (thick lines). B) Mean kERN amplitudes in a 50 ms time window (160 -210 ms, shaded area in panel A) after movement onset for very small to larger errors. Error bars represent 95% confidence intervals. C) kERN Difference waves (very small errors – large errors) for young (blue) and red (older adults) time locked to movement onset.

In order to further investigate age-related differences in trajectory error processing, we subsequently calculated difference waves between the very small error trials and the large error trials. The grand average ERP contained a peak at about 185 ms after movement onset for young adults (Figure 6C). Notably, this is about 80 ms later than classic ERN latencies typically reported for speeded choice response tasks (Nieuwenhuis et al., 2004), in which errors are binary in nature and errors can be



evaluated by use of the efference copy signal alone. The longer latency of our  $\Delta kERN$ s can be explained by its dependency on the arrival of visual and/or proprioceptive feedback, which is required to evaluate the discrepancy between the expected and actual sensory consequences (Anguera et al., 2009; Torrecillos et al., 2014).

The  $\Delta kERN$  peak was significantly different from zero in young adults (one sample t-test on adaptive mean amplitudes:  $T(24) = -5.176$ ,  $p = .001$ ). In older adults, a similar  $\Delta kERN$  was not apparent at the group level (see Figure 6). Specifically, in older adults the EEG activity time-locked to the movement onset did not scale with error size ( $p = .754$  Figure 5B), nor did the adaptive mean amplitudes of the  $\Delta kERN$  difference wave peak differ from zero ( $p = .95$ , Figure 6C). Consequently, the  $\Delta kERN$  difference wave peaks were larger in young than older adults (main effect of age,  $F(1,46) = 14.991$ ,  $p < .001$ ,  $\eta_p^2 = .246$ ). By contrast,  $\Delta kERN$  peak latency did not differ between age groups.

The fact that older adults did not reliably show a  $\Delta kERN$  at the group level suggests an age-related reduction in sensitivity to trajectory errors. However, visual inspection of older participants' movement onset locked EEG data indicates variability in  $\Delta kERN$ s, and reveals that some older adults generated  $\Delta kERN$ s, of comparable size to the young adults (see Figure 7A).

### **Aim 3: Interrelation between error processing and behavioural performance**

Our results so far confirm age-related differences in trajectory error and task error processing, as indicated by reduced  $\Delta kERN$  and  $\Delta fERN$  amplitudes for older adults. In order to further investigate the role of error processing for force field adaptation we performed robust skipped correlation analyses between the  $\Delta kERN$ ,  $\Delta fERN$ , amplitudes and the final level of adaptation separately for both groups. The final level of adaptation was calculated as the mean signed peak forces from all channel trials in the second half of the adaptation phase (bins 15-28), where performance had reached an asymptote level (see Figure 4F).

For young adults, there were no significant correlations between the final level of adaptation and any  $kERN$  or  $fERN$  difference wave amplitudes, which might be due to the fact that variance in adaptation within the group of young adults was relatively small. By contrast, for older adults we found a

medium to strong, and statistically significant, correlation between  $\Delta kERN$  difference wave peak amplitudes and final level of adaptation ( $r = -0.7013$  [CIs:  $-0.902$  ;  $-0.276$ ]; CIs reflect 98.33 % confidence intervals based on bootstrapped correlations; see Figure 7A). In other words, those older adults who showed larger (i.e. more negative and similar to young participants)  $\Delta kERN$ s, also adapted their motor commands to the force field to a greater extent. Correlations between  $\Delta kERN$  and  $\Delta fERN$  difference wave peak amplitudes were not significant, within the subgroup of older adults, when CIs were corrected for multiple comparisons ( $r = 0.445$  [CIs:  $-0.093$  ;  $0.756$ ]).

We further investigated the role of  $\Delta kERN$  on final level and rate of predictive force development using a median split approach. We divided each age group into sub-groups comprised of those with the largest and smallest  $kERN$  difference wave peak amplitudes (Figure 7b). There were no differences in any of our screening parameters (age, health, education) or the baseline performance measures between the subsamples. There were also no differences in the average sizes of errors (or error ranges) between the two subsamples for trials in each quartile used to calculate  $\Delta kERN$ , suggesting that the sizes of errors experienced by participants in the two subgroups were comparable. There were also no differences in peak velocity, distance at peak velocity or absolute reach distance in the field trials, suggesting that movement characteristics in adaptation were also comparable between subgroups. Interestingly, however, signed peak forces were larger (main effect of  $\Delta kERN$  size:  $F(1,20) = 14.279$ ,  $p < .001$ ,  $\eta_p^2 = .417$ ), signed peak errors tended to be smaller (main effect of  $\Delta kERN$  size:  $F(1,20) = 3.273$ ,  $p = .085$ ,  $\eta_p^2 = .141$ ), and movement times were faster (main effect of  $\Delta kERN$  size:  $F(1,20) = 8.155$ ,  $p = .010$ ,  $\eta_p^2 = .290$ ) for older adults with large  $\Delta kERN$ s than for older adults with small  $\Delta kERN$ s. On the contrary, there were no significant differences between the two subgroups of young adults. Significant interaction effects between bin and  $\Delta kERN$  size further suggest that predictive compensation is acquired at different rates in subsamples of older adults (Bin  $\times$   $\Delta kERN$  size:  $F(1,20) = 1.801$ ,  $p = .017$ ,  $\eta_p^2 = .083$ ). This interaction was marginal in young adults (Bin  $\times$   $\Delta kERN$  size:  $F(1,22) = 1.445$ ,  $p = .081$ ,  $\eta_p^2 = .062$ .) We further compared the rate of peak force development between sub-samples of older and young adults and confirmed that older adults with larger  $\Delta kERN$ s learned the predictive compensation for the new dynamics at a quicker rate (means

and 95% confidence interval for rate of signed peak force development in groups old  $\Delta kERN\_high = 0.427$  [CIs: 0.206, 0.655]; old  $\Delta kERN\_low = 0.0708$  [CIs: -0.030, 0.141]. Mean rates of peak force development followed a similar pattern for young adults (see Figure 7B), but the distribution of bootstrapped rate constants, does not suggest a significant differences between subgroups of young adults (means and 95% confidence interval for rate of signed peak force development in groups young  $kERN\_high = 0.319$  [CIs: -0.0578, 0.460]; young  $\Delta kERN\_low = 0.2175$  [CIs: 0.124, 0.290]).

In sum, correlation and subgroup analyses suggest that older adults who generated larger ERPs in response to reach trajectory errors adapt at a faster rate and to a larger extent than those with smaller  $\Delta kERN$ s.

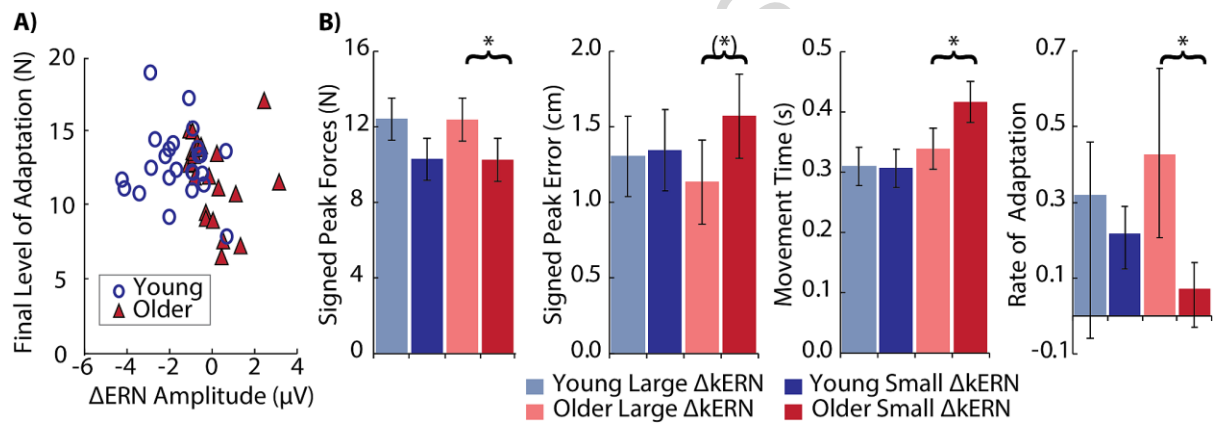


Figure 7. Interrelation between adaptation and  $\Delta kERN$ . A) Scatter plot showing the final level of adaptation and  $\Delta kERN$  for young (blue open circles) and older (red, filled triangles) participants. B) Results of median split analyses within young and older adults depending on their  $\Delta kERN$ s (light colours larger  $\Delta kERN$  groups, dark colours small  $\Delta kERN$  groups). Error bars represents 95 % confidence intervals.

## Discussion

The purpose of this study was to test how EEG markers of error processing relate to adaptation in novel dynamic movement environments, and whether this differs between young and older adults. We found that both age groups were capable of adapting reaching movements to a force field, but that the processing of both trajectory and task errors during reaching is compromised with age, as shown by a reduction in ERP responses to kinematic errors and negative task feedback. Interestingly, older people with larger neural responses to trajectory errors, that more closely resemble those of the young (more

negative ERP responses to large than to small trajectory errors, i.e. larger  $\Delta kERNs$ ), also showed greater rates and levels of adaptation to force fields. Thus, an absence of neural responses to trajectory errors can predict whether older adults have impaired capacity to adapt to novel sensorimotor conditions.

### **Young and older adults adapt similarly to force fields**

At the group level, we found no evidence of age-related differences in the rate or level of kinematic error reduction, predictive compensation of the force field or percentage of target hits, suggesting that both age groups adapted successfully. However, we found that older adults reduced their movement time when first exposed to the force field and moved slower than young adults throughout the adaptation phase (Figure 4D). The reduced movement speed, when faced with a perturbation, might reflect greater post-error slowing, an increased level of caution, and a relatively greater preference for task accuracy over speed, which are typical in older adults (Dutilh, Forstmann, Vandekerckhove, & Wagenmakers, 2013; Ruitenberg, Abrahamse, De Kleine, & Verwey, 2014; Smith & Brewer, 1995; Van Halewyck et al., 2015). Together with the finding that older adults reached peak velocity earlier and overshoot less than young adults, slower movements could also suggest greater feedback control in older adults (Seidler-Dobrin & Stelmach, 1998). Slower hand speeds would tend to reduce the perturbing force magnitude experienced by older adults, and might have contributed to reduced kinematic errors early in adaptation. However, reduced hand speed should not lead to greater predictive compensation for the robot force in channel trials, since a reduced perturbation strength should correspond to reduced adaptation magnitude. Accordingly, those older adults who slowed less adapted more (spearman robust correlation between slowing and final level of channel trial adaptation:  $r=0.580$  [95% CIs = 0.208, 0.77]). From that, and the findings that older adults with larger  $\Delta kERNs$  adapt at a greater rate and to a greater extent but also moved faster than older adults with smaller  $\Delta kERNs$  (Figure 7B), it seems that slowing is rather non-functional and non-beneficial for adaptation outcomes in older adults, which is in line with findings for sequential actions (Ruitenberg et al., 2014).

Furthermore, it is important to note that the null effect should not be interpreted as proof of adaptation equality between age groups. There was larger between-subject variability among older adults than young adults, implying that only some older adults adapted successfully to the altered dynamics, while others struggled to adapt. Increased between-subject variability is common for older adults in cognitive and motor tasks (Bock & Girgenrath, 2006), and might explain the discrepant results of the two studies that previously measured predictive compensation to force fields in older people (Huang & Ahmed, 2014; Trewartha et al., 2014). Our findings emphasise the importance of an individual differences approach to motor control and aging research; a concept that is well established in the field of cognitive aging (e.g. Salthouse, 2017).

### **Error processing during force field adaptation**

The negative EEG response to kinematic trajectory errors increased with increasing trajectory error size in young adults, presumably reflecting the magnitude of the mismatch between the predicted and experienced sensory consequences of one's actions. Thus, our results complement previous findings in young adults showing that kinematic errors caused by visuomotor distortion (Anguera et al., 2009; Vocat, Pourtois, & Vuilleumier, 2011), and unpredictable external force perturbations (Torrecillos et al., 2014), are reflected in the size of an error-related negativity component. The dorsal anterior cingulate cortex (dACC) is a key generator of the ERN and fERN in cognitive tasks (Hoffmann & Falkenstein, 2011; Walsh & Anderson, 2012) as well as motor tasks (Grafton, Schmitt, Van Horn, & Diedrichsen, 2008; for review see Seidler, Kwak, Fling, & Bernard, 2013; Torrecillos et al., 2014). This brain area contributes to error-detection, feedback and feedforward control during sensorimotor adaptation (Anguera, Russell, Noll, & Seidler, 2007; Danckert, Ferber, & Goodale, 2008; Grafton et al., 2008; Werner, Schorn, Bock, Theysohn, & Timmann, 2014), and would therefore appear to be a prime candidate for the origin of the ERN signals measured here.

Previous reductions in error-related brain potentials (ERN, and fERN) in older adults during cognitive tasks (Falkenstein et al., 2001; Nieuwenhuis et al., 2002) have been attributed to reduced dopamine levels within the midbrain dopamine system that projects to ACC (Bäckman, Lindenberger, Li, & Nyberg, 2010; Kaasinen et al., 2000; Li, Lindenberger, & Sikström, 2001; Reeves, Bench, & Howard,

2002). To the best of our knowledge, this is the first study to investigate EEG correlates of error processing during sensorimotor adaptation in older people. The similarity in age effects on error-related brain potentials measured in our motor task and previous cognitive tasks raises the possibility that aging results in a generalised impairment in error processing due to reduced dopamine availability in ACC. Alternatively, but not mutually exclusively, impaired error encoding upstream of the ACC could underpin age-related reductions in  $\Delta kERN$  and  $\Delta fERN$  amplitudes. For instance, in the current study we cannot fully rule out the possibility that older adults have impaired visual or proprioceptive acuity and processing speed, and consequently are less able to perceive kinematic errors. In addition, it is possible that due to faster and more accurate visual processing in young adults, their  $\Delta kERN$  might be more strongly affected by visual feedback. However, given that the age-related reduction of  $\Delta kERN$  and  $\Delta fERN$ , is in agreement with the well described age-effect on ERN and fERN components in cognitive tasks, we think that it is unlikely that the effects observed here are purely a by-product of age-related changes in perceptual encoding or reliance on visual feedback.

### **Trajectory error processing is crucial for adaptation outcomes in older adults**

Older adults with larger  $\Delta kERN$ s adapted quicker, and to a greater extent, than those with small  $\Delta kERN$ s. One possibility is that preserved error processing in high performing older adults indicates general maintenance of healthy brain function that is not specific to adaptation (Lee, Tan, & Qiu, 2016). However, if this were the case, there should also have been correlations between feedback processing (i.e.  $\Delta fERN$ ) and adaptation. Given that outcome error processing was *not* predictive of the ability of older people to adapt, some questions arise: (1) why are neural responses to trajectory errors but not outcome errors related to adaptation outcome in older adults? And, (2) what could be specific about error processing within the ACC that it is crucial for older adults but less important for younger adults?

Task errors can drive the changes in motor commands needed to increase task success following some forms of sensorimotor perturbation (e.g. Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015; Taylor et al., 2013), but trajectory errors seem pivotal for automatic recalibration of sensorimotor transformations (Butcher & Taylor, 2017; Izawa & Shadmehr, 2011; Shadmehr et al., 2010). Our

primary measure of adaptation, obtained via channel probe trials, reflects the extent to which participants recalibrated their feedforward motor commands to cancel the novel force field. Our findings therefore provide further evidence that trajectory errors are of greater importance for sensorimotor adaptation than task errors, presumably because trajectory errors entail important information about the direction of error (Butcher & Taylor, 2017) and the dynamics of the perturbation.

The brain activation of older adults with larger  $\Delta kERNs$  scaled with the size of trajectory errors (i.e. relatively more negative EEG response to larger as compared to smaller errors, and hence larger  $\Delta kERNs$ ), as also observed for young adults in our study and previously (Anguera et al., 2009; Torrecillos et al., 2014; Vocat et al., 2011). We speculate that this modulation of  $kERN$  amplitudes with error size might reflect a graded activation response within dACC. The overarching function of dACC is to deploy cognitive control via its interactions with the lateral prefrontal cortex (for review see Kolling, Behrens, Wittmann, & Rushworth, 2016). Greater functional as well as structural connectivity between dACC and other key regions involved in sensorimotor adaptation to visual perturbations were further associated with faster early adaptation, when the task is more cognitively demanding (Cassady et al., 2017). Here, a graded response to errors of different sizes might therefore allow cognitive control mechanisms to be allocated to facilitate force field adaptation. Recruitment of additional cognitive resources in older adults is a common finding in cognitive and motor tasks, and reflects a neural compensatory mechanism in order to maintain performance (for reviews see Reuter-Lorenz & Park, 2010, 2014; Sala-Llloch, Bartrés-Faz, & Junqué, 2015). A reduced ACC modulation with age has been shown in other tasks, including speech comprehension (Erb & Obleser, 2013), and selective attention (Milham et al., 2002), and is thought to reflect a decrease in the effectiveness of mechanisms responsible for implementing attentional control (Milham et al., 2002). The fact that adaptation is impaired in older adults with smaller  $\Delta kERNs$  raises the possibility that the selective engagement of cognitive control associated with ACC activity is pivotal for successful sensorimotor adaptation in older age. In other words, we speculate that older adults with difficulties engaging cognitive control adapt less successfully. This interpretation would be consistent with previous

observations showing that older adults have greater difficulties in engaging explicit strategies in adaptation (Hegele & Heuer, 2013; Heuer & Hegele, 2008, 2014; Heuer et al., 2011; King et al., 2013).

Young adults demonstrated successful adaptation irrespective of  $\Delta kERN$  amplitude, and it is clear that some young participants did not show larger  $kERNs$  to larger errors ( $\Delta kERNs > 0$  in some young adults, see Figure 7a). We speculate that young adults might sufficiently engage alternative resources for error encoding, including the posterior parietal cortex (PPC) (Della-Maggiore, Malfait, Ostry, & Paus, 2004) and the cerebellum (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012; Popa, Streng, Hewitt, & Ebner, 2016; Seidler et al., 2013; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007), and are therefore less dependent on graded response to errors within ACC and prefrontal processing (Christou, Miall, McNab, & Galea, 2016). Nonetheless, the general pattern of results on median split comparisons based on the size of  $\Delta kERNs$  was qualitatively similar for older and young adults (see Figure 7 b). It is important for us to emphasise that although a significant correlation was found in older but not in young adults, differences in the profile of correlation between EEG and behaviour between age groups cannot be concluded. By contrast we think that the current data provide tentative support for the possibility that selective engagement of cognitive control might also benefit young adults in force field adaptation, however further work is needed to support this notion.

#### **Alternative explanations and methodological considerations**

In older adults, larger  $\Delta kERN$  were associated with more youth like behaviour in force field adaptation (faster movement times, and larger and quicker adaptation). We think that these findings suggest that kinematic error processing and selective engagement of cognitive control is crucial for successful adaptation, especially in older adults. Nevertheless, one might ask whether these effects really are a matter of age, or whether there might be any alternative explanations. More specifically: are there factors other than age that could cause the observed differences between groups? Several between group differences in  $\Delta kERN$  occurred in parallel with between group differences in movement times. Older adults moved slower and had a larger within-subject variability in their movement times than young adults. Together, this could imply that smaller  $\Delta kERNs$  are an



epiphenomenon of slower movement time and larger movement time variability. As we time-locked the EEG to the movement onset the average ERP might be more “smeared” in older than young adults, and therefore smaller. In order to further investigate the interrelation between variability in movement time and  $\Delta kERN$  amplitudes, we conducted an additional correlation analyses between intra-individual variability in movement time (determined as the coefficient of variation of movement times in all field trials), and  $\Delta kERN$  amplitudes. If intra-individual movement time variability led to smeared and hence smaller kERNS, we would expect to see a positive correlation between these two measures (note that smaller  $\Delta kERN$ , are reflected in larger values, as this is a negative component). The results do not support the assumption: In young adults the opposite relation was revealed (i.e. larger variability in movement time was associated with larger kERNS:  $r = -.415$ ,  $p = .039$ ), and in older adults the correlation was not significant. In addition, if kERNS were only smaller because of the smearing and not due to the age-related changes in reduced dopamine levels within the midbrain dopamine system that projects to ACC, we would not expect to see any age-related differences in fERNS. For fERNS smearing is unlikely due to the abrupt feedback onset. Thus, while we cannot fully rule out this alternative, we think that smearing is unlikely to be the only reason for the differences between groups in terms of  $\Delta kERN$ .

Another methodological consideration is that we set out to investigate neurophysiological markers of error processing in young and older adults during adaptation and thus to extend previous research in young adults employing random non-learnable force perturbation schedules (Torrecillos et al., 2014). Naturally, investigating error processing during sensorimotor adaptation means that measures of error processing could be confounded by time or adaptation state. Participants experienced more frequent large trajectory errors and negative task feedback early in adaptation, and more frequent small trajectory errors and positive task feedback at the end of adaptation. Thus, our ERP measures are not only influenced by error size and task feedback valence, but also by time. Importantly, this was the same for both young and older adults and is inherent to the design employed in the current study. A promising approach for future work that allows assessment of error processing during adaptation would be the use of single trial adaptation schedules (e.g. Herzfeld, Vaswani, Marko, & Shadmehr,

2014; Marko, Haith, Harran, & Shadmehr, 2012). Such an approach affords the opportunity to study age-related differences in the responses to sensory prediction errors caused by the adaptation task in the absence of cumulative time confounds.

In addition, we do not know whether the pleasant sound might have served as an external reward. Consequently, the EEG response time locked to the onset of the feedback might not only reflect pure feedback processing, but also reward processing. Importantly, however any feedback about success or failure could be interpreted as reward, and it is impossible to know to what extent different feedback types are treated in terms of reward. Moreover, even if no external feedback were provided other than the location of the cursor with respect to the target, information about the task success could be intrinsically rewarding. Thus, it seems that feedback processing is unavoidably intertwined with reward processing in goal-directed motor tasks.

At last, as we allowed participants to practice until they felt comfortable with the task and until they successfully managed to move within the given speed constraints, there might have been differences in the number of practice trials between age groups. We did not record the number of practice trials, but from the experimenters recollection older adults were more likely to request additional practice. One might argue that any difference in the number of training trials between age groups might have disguised age-related differences in the baseline phase. However, as the primary purpose of the study was to investigate age-related differences in adaptation, we deemed it more important that all participants were equally capable of performing the task before being exposed to the perturbation. The fact the young and older adults reached a similar hit rate at baseline shows that this was the case.

### **Summary and Conclusion**

In summary, our data show that the kERN provides a marker of kinematic error-processing in force field adaptation, and that larger ERNs in response to kinematic errors are associated with better force field adaptation in older adults. We suggest that older adults with impaired capacity for encoding kinematic errors might not effectively engage cognitive control when exposed to novel mechanical

conditions, and consequently have an impaired capacity to adapt their movements to a novel dynamic environment. Thus, the extent to which neural responses to trajectory errors scale with error magnitude, or lack thereof, might serve as a predictor for adaptation impairments in older people.

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## **Greater neural responses to trajectory errors are associated with superior force field adaptation in older adults**

### **Highlights**

- Both young and older adults were capable of adapting reaching movements to a force field
- EEG responses to trajectory errors and task errors were reduced in the older group
- Larger neural responses to trajectory errors related to adaptation in older adults
- Capacity to evaluate errors might serve as a predictor for adaptation impairments

ACCEPTED MANUSCRIPT