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

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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 ($N = 24$/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.

1. Introduction

Sensorimotor adaptation is an error-based learning process (Izawa and 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 et al., 2013). Typical paradigms to study adaptation in the upper limbs are visuomotor rotation (Cunningham, 1989; Krakauer, 2009) and force field adaptation (Shadmehr and 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 and 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 et al., 2003; Hegele and Heuer, 2013; Heuer and Hegele, 2008, 2014; Heuer et al., 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 et al., 2008; Huang and Ahmed, 2014; Trewartha et al., 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

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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 et al., 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 and Shadmehr, 2011). In this paradigm, sensory prediction errors (also referred to as low level errors, see Krigolson and 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 and 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 and Shadmehr, 2011; Nikooyan and Ahmed, 2015; Taylor et al., 2013). However, the processing of sensory prediction errors seems to drive the 'true' adaptation that reflects predictive compensation for the new dynamics (Butcher and Taylor, 2017; Izawa and Shadmehr, 2011; Shadmehr et al., 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 et al., 1991) or error-related negativity (ERN; Gehring et al., 1993), and a similar negativity to negative task feedback, referred to as feedback related negativity Miltner (fERN/FRN; Miltner et al., 1997). Both ERN and fERN are reduced in older adults (e.g. Band and Kok, 2000; Falkenstein et al., 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 and 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 et al., 2017; Park and 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 and 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.

2. Methods

2.1. 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 et al., 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 < 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 et al., 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 ± 2.0 years) and 24 older participants (8 females, mean age of 69.67 ± 4.3 years). Final samples did not differ with regard to their subjective rating of health (young: 2.64 ± 0.78; older: 2.26 ± 0.79; a higher score indicates better health rating), or handedness (young: 0.79 ± 0.14; older: 0.77 ± 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 ± 5.2 years) than the younger adults (13.2 ± 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