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Older adults display diminished error processing and response in a continuous tracking task

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Abstract

Advancing age is often accompanied by a decline in motor control that results in a decreased ability to successfully perform motor tasks. While there are multiple factors that contribute to age-related deficits in motor control, one unexplored possibility is that age-related deficits in our ability to evaluate motor output result in an increase in motor errors. In line with this, previous work from our laboratory demonstrated that motor errors evoked an error-related negativity (ERN)—a component of the human ERP associated with error evaluation originating within the human medial-frontal cortex. In the present study, we examined whether or not deficits in the medial-frontal error evaluation system contribute to age-related deficits in motor control. Two groups of participants (young, old) performed a computer-based tracking task that paralleled driving while EEG data were recorded. Our results show that older adults committed more behavioral errors than young adults during performance of the tracking task. An analysis of our ERP data revealed that the amplitude of the ERN was reduced in older adults relative to young adults following motor errors. Our results make an important extension from previous work demonstrating age-related reductions in the ERN during performance of cognitive tasks. Importantly, our results imply the possibility of understanding motor deficits in older age.

KEYWORDS
EEG/ERP, error processing, feedback negativity, older adults, young adults

1 | INTRODUCTION

Many activities that we perform require responding to stimuli presented, learning from the result, and adjusting future movements. Often, we must attend and process complex stimulus presentations, detect errors, and adjust motor plans for future instances when a response is required. Indeed, these steps are critical for adaptive behavior (Hoffmann & Falkenstein, 2011). For example, operating any motorized vehicle is a complex task, involving the cooperation of many perceptual cognitive and motor control systems. Failure of any of these systems may have serious consequences. Generally, cognitive functions decline with age (Hedden & Gabrieli, 2004), and error processing appears to change across the lifespan (Hoffmann & Falkenstein, 2011). Indeed, research by Langford, Methorst, and Hakamies-Blomqvist (2006; also see Langford, Bohensky, Koppel, & Newstead, 2008) found older drivers were more frequently involved in automotive crashes in comparison to younger drivers if distances driven were more than 3,000 km. More recently, Bélanger, Gagnon, and Stinchcombe (2015) demonstrated that older adults crashed more frequently than young and middle-aged adults while distracted, despite a maintained lower average speed than the other two groups. But, this was only true if any potential corrections required simultaneous steering and braking during a short period of time. It must be noted, however, that when a single response was required to avoid a crash, older adults responded appropriately (Bélanger et al., 2015; also see Thompson et al., 2012). As the mean age of the population continues to rise, it is important to determine why older adults seem to commit errors in a variety of motor tasks (Band & Kok, 2000; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Falkenstein, Hohnsbein, & Hoormann, 1991; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Ferdinand & Kray, 2013; Hoffmann & Falkenstein, 2011). What underlying processes in the brain account for these changes in older adults?

In order to better explain why older adults commit more motor errors, it is crucial to identify and understand the factors that increase the likelihood of error commission. To successfully complete any motor task, individuals must be able to assess their environment and generate appropriate adjustments to speed and trajectory. They must also respond to novel or unexpected events such as others' behavior, and avoid obstacles or other individuals' actions. Generally speaking, adults 65 years and older commit more errors than younger adults in motor tasks (see Rusch et al., 2016). For example, work by Voelcker-Rehage, Stronge, and Alberts (2006) had younger and older participants perform a force-tracking task in the presence of a secondary cognitive (i.e., *n*-back) task using the same cognitive resources, namely, working memory. Specifically, Voelcker-Rehage and colleagues expected that force tracking performance would decline as the cognitive task complexity increased. In agreement with their hypothesis, older adults' cognitive task performance was worse than that observed in younger adults, but this was only true in a dual-task context. Furthermore, force tracking variability spiked in older adults when they had to recall an item presented once or twice in the past. In contrast, younger participants' force variability remained constant. Indeed, older adults appear to have fewer attentional resources to employ when performing dual tasks (Voelcker-Rehage et al., 2006). But, these age-related effects can be remedied with practice, albeit performance does not quite achieve the same degree as in younger adults (Voelcker-Rehage & Alberts, 2007). With respect to error commission and processing in general, it is fair to say that a reduced ability to detect and correct motor errors with age would contribute to the increased incidence of motor errors observed in older adults, as they appear to have fewer attentional resources to utilize. But, if so, what neural systems or mechanisms might help explain such effects?

A recent series of experiments have demonstrated that the human medial frontal cortex plays a key role in the evaluation of motor errors. Specifically, in a series of experiments, Krigolson and colleagues (Krigolson, Bell, Kent, Heath, & Holroyd, 2012; Krigolson & Holroyd, 2006, 2007a, 2007b; Krigolson, Holroyd, Van Gyn, & Heath, 2008) demonstrated that failure to achieve movement goals elicited error- or feedback-related negativities—EEG components of the human ERP associated with error evaluation and feedback processing, respectively. The error-related negativity (ERN; first reported by Falkenstein et al., 1990, as the error negativity or Ne, and later observed by Gehring, Goss, Coles, Meyer, & Donchin, 1993) is associated with the commission of response errors, and the feedback-related negativity (characterized by Miltner, Graun, & Coles, 1997) is evoked by performance feedback. The Ne/ERN tends to be observed at frontocentral electrode sites and localized to the anterior cingulate cortex (ACC; Debener et al., 2005; Dehaene, Posner, & Tucker, 1994; Gehring et al., 1993). fMRI supports source localization studies (Carter et al., 1998; Kiehl, Liddle, & Hopfinger, 2000; Menon, Adleman, White, Glover, & Reiss, 2001; Ullsperger & von Cramon, 2001; for reviews, see Proudfit, 2014; Taylor, Stern, & Gehring, 2007). Theoretical accounts suggest that the Ne/ERN and feedback-related negativity (fERN) reflect error and feedback evaluation by a reinforcement learning system within the human medial-frontal cortex responsible for the optimization of behavior (Holroyd & Coles, 2002, Holroyd & Yeung, 2012; Holroyd, Yeung, Coles, & Cohen, 2005; Zarr & Brown, 2016). As noted above, research by Krigolson and colleagues proposed that the medial-frontal reinforcement learning system is also responsible for the evaluation of the success or failure of a given movement—a framework they coined the hierarchical error processing hypothesis. In brief, the hierarchical error processing hypothesis posits that "high-level" outcome-related errors are evaluated by the medial-frontal reinforcement learning system (see Krigolson & Holroyd, 2007a) in order to optimize performance (i.e., motor learning). Thus, it stands to reason that deficits in a high-level error outcome system would result in reduced motor performance as one would not be able to evaluate the success or failure of movement. Importantly, previous work demonstrated diminished error processing during the performance of cognitive tasks and concomitant reductions in the amplitude of the ERN and fERN with increasing age (e.g., Eppinger, Kray, Mock, & Mecklinger, 2008). Indeed, previous reports show that older adults display reduced Ne/ERN amplitude (Falkenstein et al., 2000). Furthermore, Hoffmann and Falkenstein (2011) observed not only reduced Ne/ERN amplitude in older adults compared to young adults but the Ne/ERN displayed larger variability. In the same vein, older adults displayed slowed reaction time and diminished accuracy in a mental rotation task, along with nearly absent Ne/ERN observed in older adults despite older adults' longer reaction time compared to young adults (also see Band & Kok, 2000).

Our primary goal in the present experiment was to examine how age impacts error processing during performance of a continuous tracking task. To accomplish this, we had two groups of participants (young, old) perform a motor tracking task identical to that employed by Krigolson and Holroyd (2006) while EEG data were recorded. During performance of the task, participants were asked to manipulate a steering wheel to keep a cursor between two moving barriers without "crashing" into one of the barriers. Our hypotheses were straightforward. First, in line with previous work, we predicted crashes would evoke an error-related negativity component (Ne/ERN) associated with the evaluation of these errors. Second, we hypothesized that older participants would make more tracking errors than younger participants. Third, we hypothesized that the amplitude of the ERN evoked by crashes would be reduced in older adults.

2 | METHOD

2.1 | Participants

Twenty-six young adults (mean age: 21.4 ± 1.5, 14 females) and 26 healthy, community-dwelling older adults (mean age: 69.4 ± 2.2 years, 14 females) were recruited to participate. All participants had normal or corrected-to-normal vision with no known neurological impairments. Importantly, all older adult participants were independent community dwellers, and all were successfully able to understand and perform the task, suggesting there were no overt signs of age-related cognitive decline. The young adults were recruited from the student body of Dalhousie University and had the choice between receiving extra credit or monetary compensation (CA$20) for their participation. The older adults were recruited from the general population of the Halifax Regional Municipality using advertisements and were monetarily compensated ($20) for their participation. All participants provided informed consent, and data collection was conducted in accordance with the ethical standards prescribed in the original (1964) and subsequent revisions of the Declaration of Helsinki.

2.2 | Apparatus and procedures

We recorded EEG data from participants while they completed a custom tracking task coded in MATLAB (Version 8.6, Mathworks, Natick, MA). Participants were seated comfortably in front of a computer 19″ LCD monitor while completing the experimental task. The task consisted of thirty 2-min trials in which participants used a steering wheel to maintain the position of a cursor between two moving barriers. The barriers moved predictably back and forth to the left and right between the edges of the display separated by brief stationary periods, so-called straightaway sections, at the center of the computer display. Contact of any kind between the cursor and a barrier constituted a tracking error. If the cursor contacted one of the barriers when the barriers moved predictably, a regular tracking error occurred. Successful performance consisted of maintaining the cursor between the barriers. At a randomly selected subset of straightaway sections (20%), the barriers moved rapidly and unpredictably such that participants encountered a "difficult corner" during which the barriers would move rapidly and unpredictably to the left or to the right (equiprobable). The unpredictability of these barrier movements ensured that participants always made an error on difficult corners. On half of the difficult corners, the participant maintained full control of the cursor ("unlocked" difficult corners). On the remaining half of difficult corners, the computer program controlled the cursor and ensured that a tracking error did not occur ("locked" difficult corners). During the locked difficult corners, the amount of time the computer controlled the participant's cursor was matched on a trial-to-trial basis with the duration to barrier contact of the preceding unlocked difficult corner. This allowed a comparison of the ERP data for successful trials and trials containing errors while controlling for a general effect of surprise induced by the sudden barrier movement (see Krigolson & Holroyd 2006, 2007b, for further justification of this methodology).

2.3 | Behavioral data acquisition

The number of tracking errors for both regular tracking and difficult corners were recorded for each of the thirty 2-min trials for each participant.

2.4 | EEG data acquisition

EEG data were recorded using BrainVision Recorder software (Version 1.21, Brain Products, GmbH, Munich, Germany) and 64 electrodes that were mounted in a fitted cap with a standard 10–20 layout (ActiCAP, Brain Products). Electrodes on the cap were initially referenced to a common ground. On average, electrode impedances were kept below 20 kΩ. The EEG data were sampled at 500 Hz, amplified (ActiCHamp, Revision 2, Brain Products), and filtered through an antialiasing low-pass filter of 8 kHz. To ensure temporal coincidence of event markers with experimental stimuli, a DATAPixx stimulus unit was used (VPixx, Vision Science Solutions, Saint-Bruno, QC, Canada).

2.5 | EEG data processing

Data were processed offline with Brain Vision Analyzer2 software (Version 2.1.1, Brain Products) using methods we have previously employed (see http://www.neuroeconlab.com/data-analysis.html). First, excessively noisy or faulty electrodes were removed. The ongoing EEG data were rereferenced to an average mastoid reference and were then filtered using a dual pass Butterworth filter with a pass-band of 0.1 Hz to 30 Hz and a 60 Hz notch filter. Next, segments encompassing the onset of each event of interest (1,000 ms before to 2,000 ms after) were extracted from the continuous EEG. Following segmentation, independent component analysis (ICA) was used to correct ocular artifacts (Delorme & Makeig, 2004; Luck, 2014). Data were reconstructed after ICA, and any channels that were removed initially were interpolated using a spherical splines method. New, shorter epochs were then constructed—from 200 ms before to 600 ms after the onset of unlocked and locked difficult corners (i.e., crashes and successful tracking). Following this, all segments were baseline-corrected using a 200-ms window preceding stimulus onset. Finally, all segments were submitted to an artifact rejection algorithm that marked and removed segments that had gradients of greater than 10 μV/ms and/or a 100 μV absolute within-segment difference.

For each participant and event of interest (unlocked, locked difficult corners), ERP waveforms were created by averaging the segmented EEG data for each electrode. Subsequently, a difference waveform was created by subtracting the average regular tracking error waveforms from the average successful avoidance of collision with a barrier. For each conditional and difference waveform, a grand-averaged waveform was created by averaging corresponding ERPs across all participants. The ERN was then quantified by first identifying the time point of maximal deflection from 0 μV on the grand-averaged difference waveform in a time range and channel typically associated with the ERN for each group (younger adults: 120 ms; older adults: 150 ms; channel FCz). All peaks were then quantified on an individual basis by taking the mean voltage ± 25 ms of this time point at channel FCz. This process was identical for both groups, leaving us with ERN scores for both younger and older adults. To confirm existence of the ERN, we conducted a single-sample *t* test of the component amplitudes against zero for each group. The logic of this test is simple: if there is no difference between conditions (no ERN amplitude difference between successes and crashes, i.e., there is no component present), then the *t* test against zero will fail.

2.6 | Statistical analyses

To assess task performance, we compared the frequency of tracking errors and the amplitude of the ERN using between-subjects *t* tests. Additionally, we calculated within-group 95% confidence intervals for each group's difference waveforms.

In addition to an examination of group differences, we also wished to assess whether error processing and behavior were related regardless of age. We calculated a Pearson correlation coefficient for participant ERN amplitude and number of tracking errors—ignoring age. However, the sampling distribution of *r* was not normally distributed, and thus we used Fisher's *z* transformation. We completed this analysis to investigate individual differences in ERN amplitude (all participants: $n = 52$). We calculated a 95% confidence interval of Pearson's *r* by converting the correlation to a *z* score and calculating the *z* score standard error. We then calculated the upper and lower limit *z* scores, based on ± 1.96 *z* units, and converted them to Pearson's *r* values.

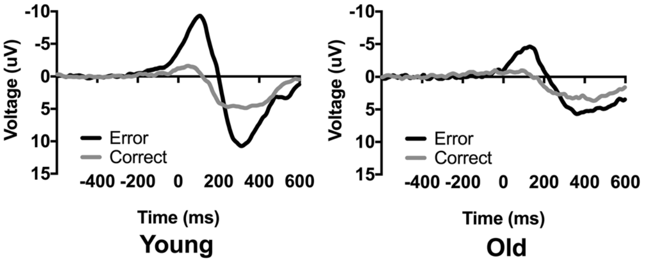

FIGURE 1 Within-group conditional waveforms at channel FCz on correct and incorrect trials. Negative values are plotted upward reflecting convention

3 | RESULTS

Given the nature of the tracking task on the locked and unlocked difficult corners, there were too few trials per condition to calculate reliable estimates of the Ne/ERN, nor was it possible to determine behavioral accuracy differences in task performance for these relatively rare events in the experiment between young and older participants. Therefore, these events were not analyzed further. However, we did analyze the frequency counts of regular tracking errors made by both groups and found that younger participants (51 [35, 66] 95% CI) made fewer tracking errors than older participants (171 [140, 202]), $t(50) = 7.168$, $p = .0013$. Our analysis of the EEG data revealed an ERP component with a scalp topography and timing consistent with the Ne/ERN[1] in both younger and older adults (see Figure 1). A comparison of ERN amplitude between younger (−9.8 uV [−7.8 uV, −11.9 uV]) and older (−5.6 uV [−4.3 uV, −6.9 uV]) adults revealed it was reduced with age, $t(50) = 3.53$, $p = .001$ (see Figure 2). Finally, we observed a statistically significant correlation between

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[1] We believe that the observed component was a feedback-related negativity (fERN), rather than a response error-related negativity (rERN), evoked by the onset of the event that caused the crash rather than the crash itself. This has been described in detail elsewhere and does not relate to the topic of the current manuscript. Thus, for simplicity's sake we have chosen to use the error-related negativity label from our original work. See MacLean et al. (2015) and our original work, Krigolson and Holroyd (2006), for more detail.

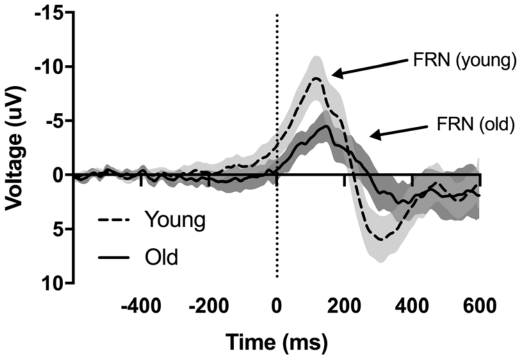

FIGURE 2 Between-group difference waveforms at channel FCz on incorrect trials. The solid line represents older adult difference wave and the dashed line represents younger adult difference wave. Shaded regions surrounding each difference wave depict 95% confidence intervals. Negative values are plotted upwards reflecting convention

ERN amplitude and the number of tracking errors made (independent of age), $r = -.450$ [−0.20, −0.64], $p = .001$ (see Figure 3). Specifically, we found that larger ERN amplitudes were associated with a smaller number of tracking errors and smaller ERN amplitudes were associated with a greater number of tracking errors.

4 | DISCUSSION

In the present study, we attempted to examine how aging impacts error evaluation in older adults. In line with previous research, we found that an ERN was evoked by errors made during the performance of a driving-related continuous tracking task. While the ERN that was observed had a longer latency than previous studies (120 ms and 150 ms, e.g., Krigolson & Holroyd, 2006), the general morphology and topography were consistent with previous accounts of the ERN (Gehring et al., 1993; see also Hofmann & Falkenstein, 2011; Vocat, Pourtois, & Vuilleumier, 2011). In terms of age-related differences, we found that older adults made more tracking errors than younger adults and, further, that the amplitude of the Ne/ERN was reduced in older relative to younger adults. We also found that there was a moderate correlation ($r = -.45$) between ERN amplitude and the number of tracking errors made, independent of age.

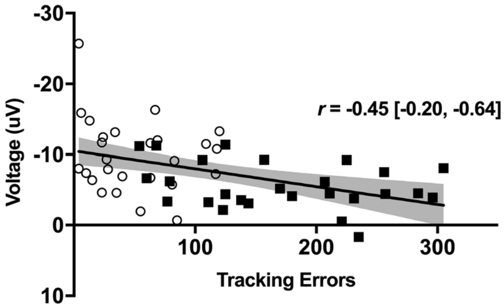

FIGURE 3 Correlation between the amplitude of the error-related negativity and the number of tracking errors made on difficult corners. Open circles represent younger adults and filled squares represent older adults. Shaded error band depicts 95% confidence interval. Negative values are plotted upwards reflecting convention

The present data support the notion that a reinforcement learning system within the medial-frontal cortex evaluates movement outcomes (Hassall, MacLean, & Krigolson, 2014; Krigolson & Holroyd, 2006, 2007a, 2007b; Krigolson et al., 2008, 2012). Previous studies of the medial-frontal system in movement outcome evaluation found that tracking errors (Krigolson & Holroyd, 2006, 2007b), aiming errors (Anguera, Seidler, & Gehring, 2009; Krigolson & Holroyd, 2007a), and postural errors (Hassall et al., 2014) evoked either an error-related or feedback-related negativity that was associated with an impairment in performance. Following from these prior results, the reduced amplitude of the ERN that we observed suggests that older adults had a deficit in their ability to identify, assess, and recover from motor errors made during the tracking task. The moderate correlation supports this idea, given that smaller mean Ne/ERN amplitude is associated with higher error frequency. In the context of the hierarchical error processing hypothesis (see Introduction), older adults appear to have a diminished capability to evaluate high-level errors (i.e., the success or failure of a given movement; see Hassall et al., 2014; Krigolson & Holroyd, 2007a).

Our results also demonstrate a correlation between average ERN magnitude and the number of errors made during task performance, suggesting a connection in the rate of error commission and the error evaluation system underlying the ERN. This increased rate of error commission and diminished ERN response to crashes may be indicative of an age-related impairment in error processing. Previous research further supports this notion of error-monitoring impairment among older adults. For example, older adults demonstrate reduced ERN magnitude in gambling tasks (Nieuwenhuis et al., 2002), as well as in spatial navigation and maze-learning tasks (Mathewson, Dywan, Snyder, Tays, & Segalowitz, 2008), relative to younger adults. Similar to evaluation of tracking errors in our paradigm, these tasks require participants to evaluate error feedback—for example, from gambling outcomes. While the timing of the ERN component in our study deviates from the timing of the feedback-related negativity observed in traditional gambling tasks, it is consistent with previous research, including visual tracking tasks (Krigolson & Holroyd, 2006) and pointing tasks (MacLean, Hassall, Ishigami, Krigolson, & Eskes, 2006; also see Vocat et al., 2011).

The ERN is thought to reflect a neural system responsible for the detection and correction of response errors (Falkenstein et al., 1990, 1991; Gehring et al., 1993; Holroyd & Coles, 2002; Holroyd et al., 2005). Previous research has localized the ERN to the ACC (Dehaene et al., 1994; Miltner et al., 1997), and theoretical accounts posit that this is the locus for response selection during task performance (Holroyd & Coles, 2002) and the evaluation of goal-related movement errors (Krigolson & Holroyd, 2007a). How is this system impacted by age? One mechanism that may contribute to deficits in this system is age-related reductions of prefrontal neural metabolic processes (Pardo et al., 2007) that could reduce the efficacy of the medial-frontal error evaluation system. Indeed, past research has demonstrated reduced ACC activity in older populations, wherein impairments in error evaluation are observed (Mathewson, Dywan, & Segalowitz, 2005; Mathewson et al., 2008). Additionally, aging is associated with a decline in midbrain dopamine uptake in rats (Cruz-Muros et al., 2009), D2/D3 receptor loss in the human brain (Kaasinen et al., 2000), and in positron emission tomography recorded from humans (Ota et al., 2006; Volkow et al., 1996, 2000). Given that the medial-frontal error evaluation is thought to be reliant on dopaminergic prediction error signals to optimize behavior (see Holroyd & Coles, 2002; Holroyd, Nieuwenhuis, Mars, & Coles, 2004; Holroyd et al., 2005), a decline in dopamine levels may further contribute to age-related impairments in error monitoring. Evidence of this has been seen in cognitive tasks, wherein the amplitude of the ERN has been found to be reduced in older participants (Wild-Wall, Willemssen, & Falkenstein, 2009). In sum, regardless of the underlying mechanism, the data from the present study suggest that age-related deficits in the medial-frontal error evaluation system contribute to the increased incidence of motor errors observed in the older population.

4.1 | Conclusions

In the present study, we found that older adults made more tracking errors and had a reduced ERN relative to younger adults. Importantly, these results suggest that a reinforcement learning system within the medial-frontal cortex responsible for evaluation of movement outcomes is impaired with age. Potentially, age-related deficits in the efficacy of the medial-frontal system might be one of the factors that contributes to the increased incidence of motor errors in the aged population.

We believe that the observed component was a feedback-related negativity (fERN), rather than a response error-related negativity (rERN), evoked by the onset of the event that caused the crash rather than the crash itself. This has been described in detail elsewhere and does not relate to the topic of the current article. Thus, for simplicity's sake, we have chosen to use the ERN label from our original work. See MacLean et al. (2015) and our original work (Krigolson & Holroyd, 2006) for more detail.

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