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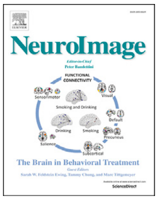

Parsing the neural signatures of reduced error detection in older age

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ABSTRACT

Recent work has demonstrated that explicit error detection relies on a neural evidence accumulation process that can be traced in the human electroencephalogram (EEG). Here, we sought to establish the impact of natural aging on this process by recording EEG from young (18–35 years) and older adults (65–88 years) during the performance of a Go/No-Go paradigm in which participants were required to overtly signal their errors. Despite performing the task with equivalent accuracy, older adults reported substantially fewer errors, and the timing of their reports were both slower and more variable. These behavioral differences were linked to three key neurophysiological changes reflecting distinct parameters of the error detection decision process: a reduction in medial frontal delta/theta (2–7 Hz) activity, indicating diminished top-down input to the decision process; a slower rate of evidence accumulation as indexed by the rate of rise of a centro-parietal signal, known as the error positivity; and a higher motor execution threshold as indexed by lateralized beta-band (16–30 Hz) activity. Our data provide novel insight into how the natural aging process affects the neural underpinnings of error detection.

Extensive research over the past three decades has established that healthy older adults exhibit declines in performance across a variety of cognitive domains (Kray and Lindenberger, 2000; Spieler et al., 2006; Verhaeghen and Cerella, 2002). Consequently, the ability to accurately monitor and evaluate ongoing performance is essential in older age to facilitate the detection of errors and the adoption of compensatory strategies. Yet, growing evidence suggests that performance monitoring itself is negatively impacted by the aging process (Harty et al., 2013; Palmer et al., 2014; Rabbitt, 1990). This is particularly concerning in light of the associations that have been documented between impaired awareness of cognitive functioning and a range of unfavorable outcomes, including engagement in risky behavior, increased care-giver burden, poor motivation for treatment and poor general prognosis (Cotrell and Wild, 1999; David, 1992; Fleming et al., 1996; Malec and Moessner, 2000; Starkstein et al., 2007). Although the effect of aging on behavioral metrics of performance monitoring have been established, the neural mechanisms mediating these changes remain poorly understood.

Electrophysiological research has largely focused on three neural signals that are thought to reflect mechanisms underpinning performance monitoring. The first of these is the error-related negativity (ERN/Ne), a fronto-centrally distributed negative waveform that has been source localized to the posterior medial frontal cortex (pMFC; Dehaene et al., 1994; Luu et al., 2004) and is seen to peak approximately 50–100 ms after an erroneous action. Various functional hypotheses have been proposed for the ERN including that it reflects a mismatch between response representations for the correct and erroneous responses (Falkenstein et al., 1999, 2000), a reinforcement learning signal (Holroyd and Coles, 2002), response conflict (Botvinick et al., 2001; van Veen and Carter, 2002) and decision confidence (Shalgi and Deouell, 2012). A common feature of these accounts is that the ERN reflects an evaluative post-response mechanism that is sensitive to negative action outcomes. More ambiguity endures regarding the extent to which the ERN is associated with explicit error detection, with several studies suggesting that it reflects preconscious mechanisms and many others suggesting that it is modulated by explicit awareness of error commission (for a review, see Wessel et al., 2011). Hereafter, we use the term error detection to refer to explicit awareness of error commission.

The second of these error-related signals is medial frontal (MF) theta (i.e. 4–8 Hz) oscillatory power, which has also been source localized to the pMFC (Luu et al., 2004). Increases in MF theta power are consistently observed around the time of response execution (Cavanagh et al., 2009; Cohen and Donner, 2013; Narayanan et al., 2013), and MF theta is particularly sensitive to variations in performance accuracy and response conflict, showing greater power for errors compared to correct trials (Narayanan et al., 2013), and for high conflict compared to low conflict trials (Cavanagh and Frank, 2014; Cohen and Donner, 2013; Cohen,

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2014). Visual inspection of error-locked time-frequency plots often suggests that error-related activity extends to lower frequencies (e.g. 2–3 Hz of the delta band). Given that this delta and theta activity is typically not fragmented in time-frequency space, authors have usually not distinguished between the contributions of each frequency band, but rather, either continue to refer to the component as MF theta (e.g. Cavanagh et al., 2009; Cohen, 2011; van de Vijver et al., 2014; Van Noordt et al., 2016), or describe it as broad theta-band range or delta/theta (Cohen, 2015; Mueller et al., 2011; Munneke et al., 2015; but see Cohen and van Gaal, 2013; Yordanova et al., 2004). There is, however, some evidence to suggest these time-frequency components may be dissociable in some circumstances (Cohen and van Gaal, 2013; Yordanova et al., 2004). We have recently demonstrated that in young adults post-error power change contiguously spanning the 2–7 Hz frequency range predicts error detection from an early latency relative to error commission, and is also highly sensitive to the timing of error detection reports (Murphy et al., 2015).

The third and final electrophysiological signal that has been linked to error detection is the late error positivity (Pe). The Pe is a slow positive waveform, which peaks 300–500 ms post-response and is maximal over centro-parietal regions. Its cardinal and unique feature is its contingency on explicit awareness of error commission, irrespective of stimulus modality and motor requirements (Nieuwenhuis et al., 2001; O'Connell et al., 2007; Murphy et al., 2012; Shalgi et al., 2009). Recently, it has also been shown that the Pe exhibits build-to-threshold dynamics that predict both the timing and probability of error detection (Murphy et al., 2012, 2015; Steinhauser and Yeung, 2012). These properties accord with proposals that error detection is a decision process that relies on the continuous accumulation of evidence that an error has been made until enough evidence has accumulated to pass an internal ‘decision threshold’ at which error detection is achieved (e.g. Steinhauser and Yeung, 2010; Ullsperger et al., 2010; Yeung and Summerfield, 2014). We have furthermore shown that the rate at which the Pe rises (hereafter, build-up rate) mediates the relationship between MF delta/theta power and the timing of error detection suggesting that MF delta/theta activity indexes an important source of modulatory input for the error decision process (Murphy et al., 2015).

To date, few studies have examined the neurophysiological mechanisms supporting error detection in healthy older adults. A number of studies have reported that the amplitudes of both the trial-averaged error-aligned ERN (Band and Kok, 2000; Beste et al., 2009; Falkenstein et al., 2001; Endrass et al., 2012; Mathalon et al., 2003; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Schreiber et al., 2011; but see Eppinger et al., 2008; Larson et al., 2016; Pietschmann et al., 2011) and Pe (Capuana et al., 2012; Clawson et al., 2017; Larson et al., 2016; Mathewson et al., 2005; Niessen et al., 2017; Staub et al., 2014) of older adults are reduced, relative to young adults. Some studies have additionally documented age-related reductions in peri-error MF delta and theta oscillations (Anguera et al., 2013; Kolev et al., 2009; van de Vijver et al., 2014). However, given that the majority of these studies did not included an overt measure of error detection it could not be determined to what extent attenuation of these components related to age-related reductions in explicit error detection per se. Two notable exceptions involved asking participants to indicate awareness of error commission with an overt response following a delay period (Niessen et al., 2017; Schreiber et al., 2011). But, as highlighted by Klein and colleagues in a recent review (Klein et al., 2013), a consequence of this approach is that any average group differences in the amplitude of the Pe may be partly, or even exclusively, due to differences in the timing of error detection, and not to failures of conscious awareness per se. These authors accordingly suggest that investigations of explicit error detection should include a speeded signaling response to obtain precise timing information about the awareness process, and avoid the amplitude being affected by a signaling latency jitter.

The manner in which recent work in young healthy adults has related error detection to a decision process provides a valuable framework for gaining a more precise understanding of the neural mechanisms underpinning the capacity for error detection in older adults, and other populations with error detection deficits (e.g. O'Connell et al., 2009). Here, we exploited this knowledge to identify the neurophysiological basis of age-related reductions in error detection using a paradigm that requires participants to overtly signal their errors via a speeded manual response. Although we have previously established that error detection on this paradigm and the corresponding neural signals are not significantly affected by stimulus-evoked and motor-related activity in young adults (Murphy et al., 2012, 2015), we were cognizant that age-related differences in sensory encoding and motor preparation may influence the likelihood and timing of error detection. Therefore, in addition to examining the ERN, Pe and MF delta/theta, we sought to assess age-related differences in visual evoked potentials (VEP) and a key motor preparation signal, lateralized beta band (16–30 Hz) activity. Given that previous research on age-related differences in motor preparation signals has almost invariably suggested that older adults require longer activation of the motor cortex to enable action execution (Cespón et al., 2013; Kolev et al., 2006; Rossiter et al., 2014; Roggeveen et al., 2007), we expected that older adults would exhibit greater pre-response lateralized beta desynchronization compared to younger adults. We additionally explored how a simple accumulation-to-bound model accounts for the age-related changes in error detection behavior.

1. Methods

1.1. Participants

Previous research examining age differences in our main variables of interest, explicit error detection (Harty et al., 2013; Schreiber et al., 2011), Pe amplitude (Mathewson et al., 2005; Capuana et al., 2012; Clawson et al., 2017; Larson et al., 2016) and MF theta power (Reichert et al., 2016; Anguera et al., 2013), have all reported medium to large effect sizes (Cohen's *d*). Based on the assumption that these effect sizes could be inflated (Button et al., 2013; Larson and Carbine, 2017), we used G*Power (version 3.1.9.2; Faul et al., 2013) to determine what sample size we would need to have 80% power to detect a *small* effect size (Cohen's $d = 0.2$), for an alpha level of 0.05. This calculation suggested that a total sample of 52 would be sufficient to detect even a small effect of age on these variables. With scope for potential loss of participants due to poor data quality or violation of a priori criteria, we collected data on 31 healthy older adults and 32 healthy young adult controls. The data from the young participants has previously been published elsewhere (Murphy et al., 2012, 2015).

All participants were right-handed, had normal or corrected-to-normal vision, had no history of color blindness, no history of psychiatric illness or head injury, and were not taking any psychoactive medications. Two older adults were excluded because their Mini-Mental State Examination (MMSE; Folstein et al., 1975) score indicated possible cognitive impairment (<24). Two older and two young adults were excluded due to poor accuracy on the task (<30% correctly withheld No-go trials). Another young adult was excluded due to technical issues with the EEG recording, and a final young adult was excluded because they had no observable Pe component. Larson et al. (2010) among others (e.g. Olvet and Hajcak, 2009) have reported that a minimum of 12 trials per participant is required to obtain a reliable signal-to-noise ratio for EEG analyses. Following artifact rejection, two older adults had less than 12 undetected error trials, and a further two had less than 12 undetected and detected error trials. These four participants were therefore excluded from the reported results. However, we confirmed that the same pattern of results was observed when the former two participants were included for the analyses that related uniquely to detected error trials. Accordingly, the reported data is based on a sample that consisted of 23 older adults (15 female) with a mean age of 71.2 (*SD* 6.38, range 65–88) and 28 younger adults (15 female), with a mean age of 23.5 (*SD* 5.8, range 18–35). All participants were asked to refrain from consuming caffeine on the day of testing. Procedures were approved by the Trinity College