Title: Disturbing standing balance evokes an error-related negativity

Short Title: Disturbing standing balance evokes an ERN

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Abstract: The error-related negativity (ERN) is a neural correlate of error monitoring often used to investigate individual differences in developmental, pathological, and adaptive contexts. However, limited experimental control over errors presents several confounds to its measurement. An experimentally controlled disturbance to standing balance evokes the balance N1, which we previously suggested may share underlying mechanisms with the ERN. We test the possibility of shared underlying mechanisms by testing whether the balance N1 and ERN are associated in amplitude across individuals within two populations across the adult lifespan (N=21 young adults and N=20 older adults). ERNs were measured in two versions of an arrow flanker task where responses were entered by the hand (ERN-hand) or feet (ERN-foot). The balance N1 was evoked by sudden slip-like movements of the floor beneath a standing participant. The ERNs and the balance N1 showed good to excellent internal consistency and were correlated in amplitude in both populations. One principal component accounted for approximately 80% of variance as being shared across the three evoked responses within each group, but the association between the ERN-hand and ERN-foot remained significant when the balance N1 was included in the model. The results suggest the balance N1 and ERN share mechanisms underlying individual differences in error monitoring. Balance perturbations may therefore provide a well-controlled method for examining individual differences in the neural system that monitors errors.

Impact Statement: The error-related negativity (ERN) is a widely investigated neural correlate of error monitoring, but its measurement is complicated by lack of experimental control over spontaneous errors. Experimentally imposed errors to upright posture evoke the balance N1, which yields excellent internal consistency and is correlated in amplitude with the ERN. Balance errors may therefore provide a well-controlled method for examining individual differences in error monitoring.

1. Introduction

The error-related negativity (ERN) is a neural correlate of error monitoring often used to investigate individual differences in developmental, pathological, and adaptive contexts, but several factors confound its measurement. The ERN is a negative deflection in frontocentral midline EEG after spontaneous mistakes in a variety of speeded forced-choice response tasks (Meyer, Riesel, & Proudfit, 2013; Riesel, Weinberg, Endrass, Meyer, & Hajcak, 2013). The ERN is thought to arise from neural circuits involving the anterior cingulate cortex and supplementary motor area (Bonini et al., 2014; Dehaene, Posner, & Tucker, 1994; Gentsch, Ullsperger, & Ullsperger, 2009). Although frequently used as a measure of individual and group differences related to psychopathology (Moser, Moran, Schroder, Donnellan, & Yeung, 2013; Olvet & Hajcak, 2008; Seer, Lange, Georgiev, Jahanshahi, & Kopp, 2016), the ERN can be confounded by task interpretation and task performance, with larger amplitudes when focusing on accuracy (Gehring, Goss, Coles, Meyer, & Donchin, 1993) and in individuals who make fewer errors (Fischer, Klein, & Ullsperger, 2017). Differences in the ERN across development (Tamnes, Walhovd, Torstveit, Sells, & Fjell, 2013) and aging (Beste, Dziobek, Hielscher, Willemssen, & Falkenstein, 2009a; Nieuwenhuis et al., 2002) can be difficult to interpret because different age groups need different tasks to maintain similar levels of engagement and difficulty in order to minimize confounds related to differences in motivation and performance accuracy (Lewis & Stieben, 2004). And while many theories implicate the ERN in adaptive behavior (Holroyd & Coles, 2002b; Ullsperger, Danielmeier, & Jocham, 2014), incremental trial-by trial adaptation is not robustly testable or readily observable in tasks with categorical response options. However, the ERN appears to reflect the activity of a generic error detection system that responds similarly to errors committed by the hand, foot (Holroyd, Dien, & Coles, 1998), or eyes (Van't Ent & Apkarian, 1999), to continuous motor errors that are independent of decision-making (Gallea, Graaf, Pailhous, & Bonnard, 2008; Maurer, Maurer, & Muller, 2015), and even after errors that are not committed by the individual if the individual is responsible for correcting the error (Gentsch et al., 2009). This flexibility in the kind of error events that engage the error monitoring system could be leveraged to develop a more ecologically relevant task that provides more experimental control over errors that elicit the ERN.

An experimentally controlled disturbance to standing balance evokes the balance N1, which we have suggested may be functionally similar to the ERN. The balance N1 is a negative deflection in frontocentral midline EEG after a balance disturbance that has been localized to the supplementary motor area (Marlin, Mochizuki, Staines, & McIlroy, 2014; Mierau, Hulsdunker, & Struder, 2015). The balance N1 was initially thought to be a sensory signal (Dietz, Quintern, & Berger, 1984a, 1984b, 1985b; Dietz, Quintern, Berger, & Schenck, 1985a), but was later recognized as an error signal because it disappears when the balance disturbance is expected (Adkin, Quant, Maki, & McIlroy, 2006). Much like the ERN, the balance N1 can be evoked in a variety of different tasks (Ackermann, Diener, & Dichgans, 1986; Adkin et al., 2006; Mochizuki, Boe, Marlin, & McIlRoy, 2010; Payne, Hajcak, & Ting, 2019a; Staines, McIlroy, & Brooke, 2001), and appears to be independent of whether the arms or legs are used to correct for the error (Mochizuki, Sibley, Cheung, Camilleri, & McIlroy, 2009a). Balance errors are intrinsically motivating, as they occur in everyday life, and evoke an involuntary balance-correcting reaction (Jacobs & Horak, 2007a) that requires no instruction on how to perform or perceive the task. This intrinsic motivation avoids potential confounds related to how the task is explained and interpreted and may also relate to why the balance N1 is so large in amplitude, being robustly observable on individual trials (Ditz, Schwarz, & Muller-Putz, 2020; Payne et al., 2019a). The better signal-to-noise ratio that comes with the large amplitude of the balance N1 also has the potential to yield better psychometric properties than the ERN. Importantly, balance errors are experimentally controllable, allowing the exact same series of errors to be repeated across individuals (Adkin et al., 2006; Welch & Ting, 2014). The balance N1 can be evoked in nearly anyone able to stand without an assistive device, from toddlers (Berger, Horstmann, & Dietz, 1990; Berger, Quintern, & Dietz, 1987) through the elderly (Duckrow, Abu-Hasaballah, Whipple, & Wolfson, 1999; Payne, McKay, & Ting, 2022; Payne, Palmer, McKay, & Ting, 2021). We previously suggested the balance N1 and ERN may arise from overlapping neural processes based on their similar dependencies on motivation, perceived consequences, perceptual salience, expectation, development, and aging (Payne, Ting, & Hajcak, 2019b). We now test the possibility of shared underlying mechanisms by testing whether the balance N1 and ERN are associated in amplitude across individuals within two populations across the adult lifespan.

We hypothesized that the balance N1 and ERN arise from shared neural mechanisms and would therefore be correlated in amplitude across individuals. We measure the ERN in two versions of an arrow flanker task (Eriksen & Eriksen, 1974) that differ in whether responses are entered by the hand or the feet. We measure the balance N1 evoked by slip-like perturbations in which the floor suddenly slides beneath a standing participant. We compare the ERNs across individuals between the two response modalities in the flanker task to establish consistency of the ERN across two objectively similar tasks. We then compare the balance N1 to the ERNs from both versions of the flanker task to assess whether the balance N1 shares variance with the individual differences reflected in the ERN. These associations were initially tested in a small sample of young adults (ages 19-38) and were then replicated in a small sample of older adults (ages 59-82) to establish stability of the associations across the adult lifespan.

2. Methods

2.1. Study 1 Methods

2.1.1. Participants

Twenty-one healthy young adults (age 25±5 years, range 19-38, 12 female) were recruited from the community surrounding Emory University. The protocol was approved by the Institutional Review Board of Emory University, and all participants were informed of the study procedures and provided written consent before participation. Different analyses of the balance N1 potential in this population are previously published (Payne & Ting, 2020a; Payne & Ting, 2020c).

2.1.2. Balance Task

Participants were exposed to a series of 48 translational support-surface balance perturbations that were unpredictable in timing and magnitude. The support-surface moved backward in all perturbations, resulting in a relative forward lean of the body (**FIGURE 1**). Three perturbation magnitudes were used to ensure unpredictability of the perturbation characteristics. The small perturbation was identical across participants (7.7 cm, 16.0 cm/s, 0.23 g). The medium (12.6-15.0 cm, 26.6-31.5 cm/s, 0.38-0.45 g) and large (18.4-21.9 cm, 38.7-42.3 cm/s, 0.54-0.64 g) perturbations were scaled by participant height to control for the effect of participant height on the balance N1 (Payne et al., 2019a) and to ensure that the more difficult perturbations were mechanically similar across body sizes. To prevent fatigue, 5-minute rest breaks were enforced when the full duration of the perturbation series was expected to exceed 16 minutes, with additional breaks allowed upon request. Not counting these breaks, the duration of the perturbation series was 17.4±16 minutes across participants. Inter-trial-intervals between perturbation onsets were 22±3 s, with perturbations manually triggered when the EEG baseline was relatively quiescent, approximately 5-15 s after the participant returned to a stable, upright posture.

Participants were harnessed to the ceiling for safety using a harness that provided no weight support during perturbations. The harness could suddenly catch a participant if they began to fall toward the ground, but this did not occur in either of the populations reported here. Participants were instructed to cross their arms in front of their chest and focus their gaze at a picture of a mountain landscape 4.5 meters ahead during the initial platform motion. On half of trials, participants were asked to recover balance by taking a single step forward. On the remaining trials, participants were asked to recover balance without taking a step, which was not always possible at the larger perturbation magnitudes. Stepping instructions were varied randomly between blocks of 6 trials, with each block containing two replicates of each perturbation magnitude in random order. Although we previously reported small differences in the balance N1 across perturbation magnitudes in some individuals (Payne et al., 2019a; Payne & Ting, 2020a), and small changes in the balance N1 with stepping at the largest perturbation magnitude (Payne & Ting, 2020c), the present analyses will collapse across all trial types to maximize and balance the number of trials included in the measurement of the balance N1.

Due to failure to save the EEG data, data from the perturbation series is unavailable for one participant.

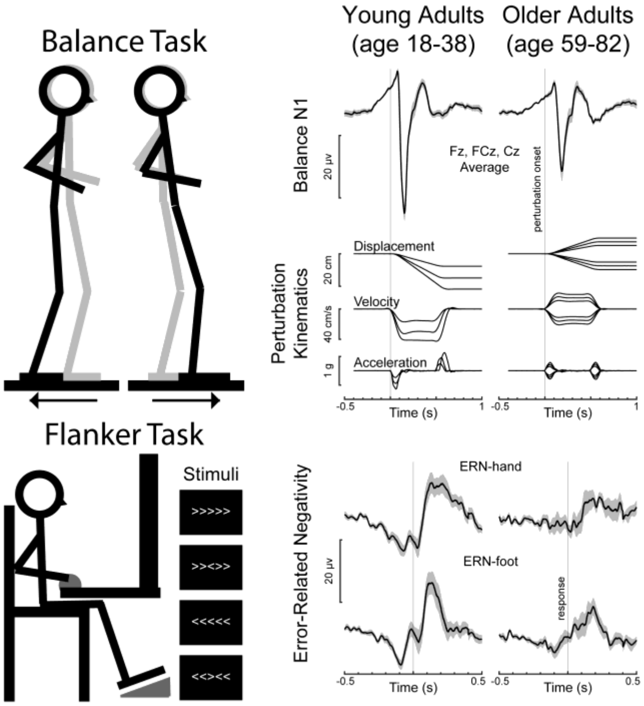


Figure 1. Experimental Tasks. (Top panel) A schematic depicts the balance task along with grand-averaged balance N1s and perturbation kinematics from young and older adult populations. (Bottom panel) A schematic depicts the flanker task, with the two response entry devices depicted in gray. Grand-averaged error-related negativities (ERNs) are shown for the hand and foot response modalities of the flanker task in both populations. ERP data in all panels is averaged across Fz, FCz, and Cz, with the standard error of the mean across participants shaded. Note that the young adults received only backward perturbations while the older adults received both backward and forward perturbations of smaller magnitude. Axes are matched to enable comparisons between young and older adults, as well as between balance and flanker ERPs.

2.1.3 Flanker Tasks

After the perturbation series and a 5-minute rest break, participants performed two versions of an arrowhead flanker task (Eriksen & Eriksen, 1974) in counterbalanced order using Presentation software (Neurobehavioral Systems, Inc., Albany, California). The two versions differed in response modality. In one version, participants responded to stimuli by clicking the left or right mouse buttons using the pointer and middle fingers of the hand of their choice. In the other version, participants responded to stimuli by releasing a foot pedal under the ball of the left or right foot, with the pedals otherwise remained pressed throughout the task. The tasks were otherwise identical with one exception that a message to “Please ensure both foot pedals are depressed” was inserted between stimuli in the foot response version if the foot pedals were not engaged at the time the next stimulus was supposed to be displayed.

In both task versions, participants were shown five arrowheads in each trial, and were instructed to respond as quickly and accurately as possible according to the direction of the central arrowhead (**FIGURE 1**). Stimuli were balanced between compatible (“>>>>>” and “<<<<<”) and incompatible (“>><>>” and “<<><<”) conditions in random order. Each stimulus was displayed for 200 ms, and the interval between offset of one stimulus and onset of the subsequent stimulus varied randomly between 2300-2800 ms, unless delayed by failure to engage foot pedals as described above. In such a case, the message would disappear once the pedals were pressed, and the next stimulus was displayed 2300-2800 ms later. Participants first completed a supervised practice block of 11 trials, which could be repeated if participants still did not understand the task. After the practice block, each task consisted of up to 11 blocks of 30 trials (up to 330 total trials), with each block initiated by the participant. The task was set to terminate early if 21 errors were obtained (Meyer et al., 2013). In attempt to maintain accuracy between 75-90%, messages were displayed between blocks stating, “Please try to be more accurate,” “Please try to respond faster,” or “You’re doing a great job,” according to the accuracy of the preceding block.

Three participants completed only the hand response version of the task and two participants completed only the foot response version of the task due to changes in the experimental protocol across the first five participants. The remaining sixteen participants completed both versions of the flanker task counterbalanced in order.

2.1.4. EEG Collection

EEG data were collected during all three tasks using a 32-channel active electrode system (ActiCAP, Brain Products, Germany) placed according to the international 10-20 system. Electrodes TP9 and TP10 were removed from the cap and placed directly on the skin over the left and right mastoid bones for offline re-referencing. Electrodes were prepared with conductive electrode gel (SuperVisc HighViscosity Electrolyte-Gel, Brain Products) using a syringe that abraded the scalp to improve impedances. Impedances at Cz and mastoid electrodes were generally below 10 kOhm before the start of data collection. Vertical EOG was collected to correct for blink and eye movement artifacts using bipolar passive electrodes (E220x, Brain Products), placed above and below the right eye with a forehead reference. EOG electrodes were prepared with high-chloride abrasive gel (ABRALYT HiCl, High-chloride-10% abrasive electrolyte gel, Brain Products). EEG and EOG data were amplified on an ActiCHamp amplifier (Brain Products) and sampled at 1000 Hz following a 24-bit A/D converter and 20 kHz online anti-aliasing low-pass filter. The EEG system also recorded data from a 3D accelerometer placed on the head to monitor for the possibility of motion artifacts during the balance task.

2.1.5. EEG Pre-Processing

EEG data were high-pass filtered at 1 Hz with forward and backward passes of third-order Butterworth filters to ensure zero lag, mean-subtracted within channels, and then similarly low-pass filtered at 25 Hz. EEG data were re-referenced to the average of the mastoids and epoched around perturbation onset for the balance perturbations, and around response entry for the flanker task (detailed below) at Fz, FCz, Cz, and the vertical EOG channel. The Gratton and Coles algorithm (Gratton, Coles, & Donchin, 1983) was applied to correct for blink and eye movement artifacts at Fz, FCz, and Cz using the vertical EOG channel. Due to limited numbers of trials within any given trial type (e.g., errors, nonstepping responses to large backward perturbations, etc.), trial types were not distinguished in the correction of eye artifacts, but data from the three tasks were processed separately.

2.1.6. Balance Task ERPs

Filtered and re-referenced EEG data from the perturbation series were epoched in the period of 400 ms before perturbation onset, defined as the onset of perturbation acceleration (**FIGURE 1**), until 2000 ms after perturbation onset. After eye artifact correction (described above), subject-averaged ERPs were created by averaging the EEG data across all trials within each participant, separately for Fz, FCz, and Cz. No perturbation trials were excluded from analysis for any reason as the signal to noise ratio of the balance N1 is larger than most typical artifacts, and a quiet baseline was manually confirmed prior to perturbation onset. Additionally, due to the nature of the perturbations applied at the feet, significant head motion did not occur until after the balance N1 (**FIGURE 2**), and thus head acceleration data were not assessed further. The balance N1 was quantified as the most negative amplitude in subject-averaged ERPs between 100-250 ms after perturbation onset relative to the mean of a baseline period of 50-150 ms before perturbation onset.

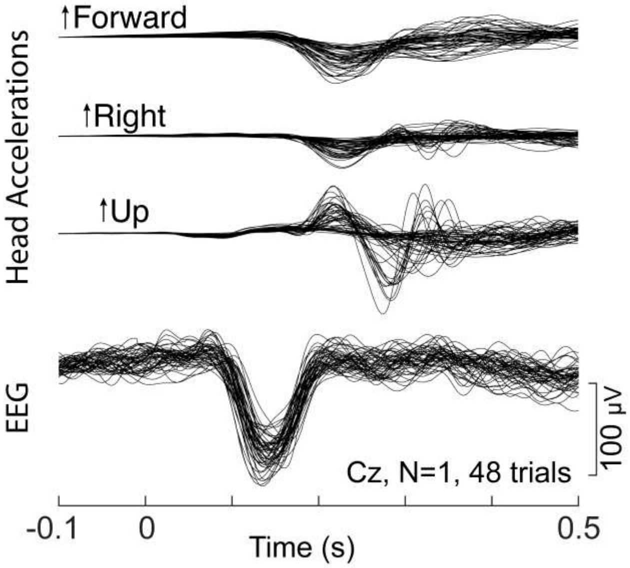


Figure 2. The balance N1 is not a motion artifact. 3D head accelerations and balance N1s are shown for all trials in the balance task from one example participant in the young adult group. Note that head accelerations to the left in this example arise from anticipatory postural adjustments preceding a step to recover balance with the right foot.

2.1.7 Flanker Task ERPs

EEG data were processed separately for hand and foot response versions of the flanker task. Filtered and re-referenced EEG data were epoched in 1000 ms segments centered on response entry at Fz, FCz, and Cz. Trials were discarded from analyses according to the following automated rejection criteria: <0.5 µV difference for over 100ms, >50 µV difference between consecutive samples, >300 µV difference across the epoch, reaction times more than 3 standard deviations from the participant's average reaction time, within-trial range in voltage more than 2 standard deviations above the participant's average, or within trial variance across samples more than 2 standard deviations above the subject's mean. Subject-averaged ERPs were created using the remaining error trials, separately at Fz, FCz, and Cz. To mimic the scoring approach of the N1, the ERN was measured in the ERP from error trials as the most negative point between 50 ms before response to 100 ms after response relative to the average of a baseline of 300-500 ms prior to response entry. Similar results were obtained when ERPs were measured as the mean of a 50 ms window centered around the peak. For simplicity, ERNs from the two different response modalities will be referred to as the ERN-hand and the ERN-foot.

All of the young adults had at least six artifact-free error trials, and thus no young adults were excluded for an insufficient number of error trials.

2.1.5. Statistical Analyses

Internal Consistency was assessed in terms of the split-half reliability**.** Split-half reliability was assessed by comparing the amplitudes of the ERPs created by separately averaging the even and odd trials that went into the subject averages. Specifically, the split-half reliability was taken as the Pearson's correlation coefficient between the amplitudes measured from the even and odd averaged waveforms across participants, which was subsequently corrected using the Spearman-Brown prophecy formula (Cassidy, Robertson, & O'Connell, 2012; Warrens, 2017).

Pearson product-moment correlations were used to test for associations between the ERN-hand and ERN-foot. Similarly, Pearson product-moment correlations were used to test for associations between each of these ERNs and the balance N1. Variables deviating from a normal distribution (Shapiro-Wilk $p<0.05$) were transformed to a normal distribution using boxcox.m in MATLAB (MathWorks Inc.) prior to calculation of statistics. Scatter plots display original, untransformed data values along with corrected statistics as appropriate.

A principal component analysis (PCA) was used to measure the variance shared across the three ERPs. Specifically, PCA (pca.m in MATLAB) was applied to the three ERP amplitudes at the Fz electrode, where associations across the ERPs were greatest. The variables were scaled to unit variance before PCA to balance the contributions of each ERP. Missing data were handled using the alternating least squares algorithm ('ALS' option in pca.m), enabling inclusion of all participants, even those who did not complete all three tasks. As the largest principal component loaded all three ERPs, the proportion of the total variance accounted for by that component was used as a measure of the variance shared across the three ERPs. Additionally, to assess whether there was variance unique to the ERNs that was not shared with the balance N1, we performed a multiple regression analysis where the ERN-foot and the balance N1 were entered as simultaneous predictors of the ERN-hand at the Fz electrode.

2.2. Study 2 Methods

2.2.1. Participants

Twenty healthy older adults (age 70±7 years, range 59-82, 7 female) were recruited from the community surrounding Emory University. The protocol was approved by the Institutional Review Board of Emory University, and all participants were informed of the study procedures and provided written consent before participation.

Unless specified below, all methods and procedures were identical to Study 1. One older adult was unable to perform either version of the flanker task due to inability to perceive the brief 200 ms stimuli. Another older adult was excluded from analyses for near chance accuracy (53% accuracy in hand version, 47% accuracy in foot version), and an additional two older adults were excluded from analyses of the ERN-hand due to fewer than 6 artifact-free error trials. Additionally, due to poor signal quality at Cz (resulting from repeated electrode pop-off during the experimental session), data at the Cz electrode was replaced with the average of electrodes C1 and C2 in one individual across all three tasks.

2.2.2 Balance task

Participants were exposed to a series of 48 translational support-surface balance perturbations that were unpredictable in timing, magnitude, and direction. Perturbations were balanced between forward and backward perturbation directions, and between three perturbation magnitudes in block-randomized orders (**Figure 1**). The small perturbation was identical across participants (5.1 cm, 11.1 cm/s, 0.15 g), while the medium (7.0-7.4 cm, 15.2-16.1 cm/s, 0.21-0.22 g) and large (8.9-9.8 cm, 19.1-21.0 cm/s, 0.26-0.29 g) perturbations were scaled according to participant height. A 5-minute break was enforced half-way through the perturbation series, with additional breaks allowed upon request. Not counting breaks, the perturbation series lasted 18±2 minutes, and inter-trial intervals between perturbation onsets were 23±10 s.

2.2.3 Statistical analyses

All analyses were performed as described in Study 1, with the exception of the PCA and multiple regression analysis, which focused on the Cz electrode in the older adults, where associations across their ERPs were strongest.

In addition to the analyses described in Study 1, we also used one-tailed *t*-tests to assess whether ERNs were smaller in the older adults compared to the younger adults to establish consistency with existing studies (Beste, Willemssen, Saft, & Falkenstein, 2009b; Nieuwenhuis et al., 2002). While the balance N1 is also smaller in older adults (Duckrow et al., 1999), a similar comparison in the present data would be confounded by the smaller perturbation magnitudes in the older group. Although the same balance perturbations could have been used between the young and older adult groups, these studies were originally designed to address different experimental questions related to the balance N1 potential (Payne et al., 2022; Payne et al., 2021; Payne & Ting, 2020a; Payne & Ting, 2020c).

3. Results

3.1. Study 1 Results

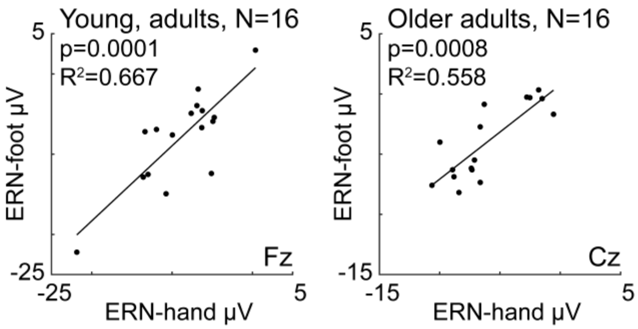
In the hand version of the flanker task, young adults (N=19) committed an average of 19±3 errors, with 90±4% accuracy, and reaction times of 385±23 ms (errors 337±35 ms, correct 391±24 ms). After trial rejections, 17±3 error trials were included in the measurement of the ERN-hand (Fz 16±3, FCz 17±3, Cz 17±3). ERN-hand amplitudes were -9.3±5.5, -9.1±3.8, and -7.0±3.2 µV at Fz, FCz, and Cz. In the foot version of the flanker task, young adults (N=18) committed an average of 21±2 errors, with 89±4% accuracy, and reaction times of 405±35 ms (errors 331±26 ms, correct 414±36 ms). After trial rejections, 17±2 error trials were included in the measurement of the ERN-foot (Fz 16±3, FCz 17±2, Cz 18±2). ERN-foot amplitudes were -7.5±5.7, -7.4±5.3, and -6.3±4.6 µV at Fz, FCz, and Cz.

ERNs showed good reliability and were associated in amplitude across the hand and foot flanker tasks. Split-half reliabilities at Fz, FCz, and Cz were 0.90, 0.86, and 0.79 for the ERN-hand, and 0.86, 0.84, and 0.80 for the ERN-foot. The ERN-hand and ERN-foot were associated in amplitude across the young adults (**FIGURE 3**, N=16, Fz p=0.0001 R^2=0.667, FCz p=0.055, Cz p=0.33).

The balance N1 showed excellent reliability and was associated in amplitude with the ERNs. Balance N1 amplitudes in the young adults (N=19) were -28.1±9.6, -43.8±12.5, and -54.1±18.0 at Fz, FCz, and Cz. Split-half reliabilities at Fz, FCz, and Cz for the balance N1 were 0.94, 0.98, and 0.99. Balance N1 amplitudes were associated with the ERN-hand (**FIGURE 3**, N=18, Fz p=0.0059 R^2=0.386, FCz p=0.0317 R^2=0.257, Cz p=0.062) and the ERN-foot (N=17, Fz p=0.00048 R^2=0.567, FCz p=0.0204 R^2=0.310, Cz p=0.224).

Variance was shared across the three ERPs, with additional variance specific to the flanker ERNs. A single principal component accounted for 81% of the variance across the three ERPs at the Fz electrode in the young adults. However, a significant association between the flanker ERNs persisted at Fz (p=0.025) when the balance N1 was included in the model.

A. Comparisons between Flanker tasks



B. Comparisons between Balance and Flanker tasks

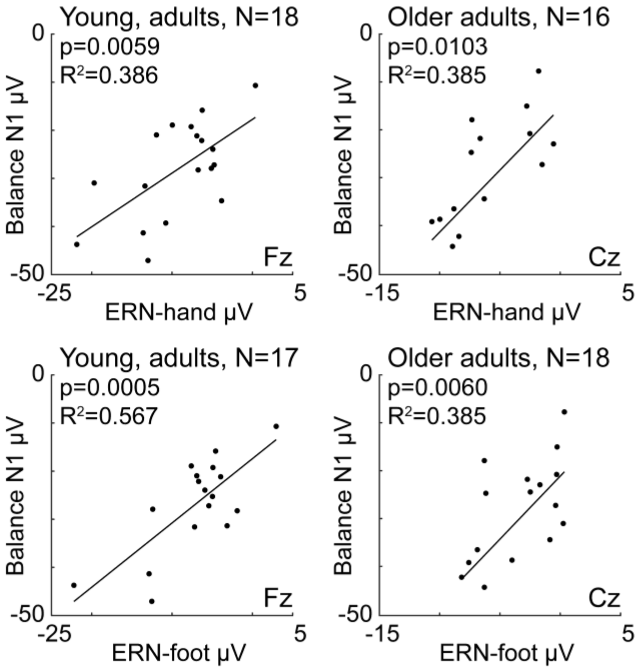


Figure 3. Associations in ERPs across tasks. (A) Scatter plots show associations in the error-related negativity (ERN) between the hand and foot response versions of the flanker task. (B) Scatter plots show associations between the balance N1 and the ERNs from the hand and foot response versions of the flanker task.

3.2. Study 2 Results

In the hand version of the flanker task, older adults (N=16) committed an average of 16±5 errors, with 93±4% accuracy, and reaction times of 503±149 ms (errors 459±298 ms, correct 509±144 ms). After trial rejections, 16±5 error trials were included in the measurement of the ERN (Fz 13±5, FCz 14±5, Cz 14±5). ERN-hand amplitudes were -5.3±4.5, -6.1±3.0, and -6.1±3.2 µV at Fz, FCz, and Cz. In the foot version of the flanker task, older adults (N=18) committed an average of 21±1 errors, with 85±7% accuracy, and reaction times of 462±58 ms (errors 359±51 ms, correct 482±60 ms). After trial rejections, 18±2 error trials were included in the measurement of the ERN-foot (Fz 17±3, FCz 18±2, Cz 18±2). ERN-foot amplitudes were -4.7±4.6, -4.0±3.3, and -3.7±3.1 µV at Fz, FCz, and Cz.

ERNs showed good reliability at most sites and were associated in amplitude across the hand and foot flanker tasks. Split-half reliabilities at Fz, FCz, and Cz were 0.89, 0.88, and 0.70 for the ERN-hand, and 0.87, 0.88, and 0.88 for the ERN-foot. The ERN-hand and ERN-foot were associated in amplitude across the older adults (**FIGURE 3**, N=16, Fz p=0.243, FCz p=0.011 R^2=0.378, Cz p=0.00081 R^2=0.558).

The balance N1 showed excellent reliability and was associated in amplitude with the ERNs. Balance N1 amplitudes in the older adults (N=20) were -22.6±11.5, -29.7±13.0, and -32.9±14 at Fz, FCz, and Cz. Split-half reliabilities at Fz, FCz, and Cz for the balance N1 were 0.98, 0.96, and 0.99. Balance N1 amplitudes were associated with the ERN-hand (**FIGURE 3** N=16, Fz p=0.704, FCz p=0.092, Cz p=0.0103 R^2=0.385) and the ERN-foot (N=18, Fz p=0.109, FCz p=0.00491 R^2=0.542, Cz p=0.0060 R^2=0.385).

Variance was shared across the three ERPs, with additional variance specific to the flanker ERNs. A single principal component accounted for 78% of the variance across the three ERPs at the Cz electrode in the older adults. However, a significant association between the flanker ERNs persisted at Cz (p=0.023) when the balance N1 was included in the model.

4. Discussion

The observed correlations support the hypothesis that the balance N1 and ERN share underlying neural mechanisms. The balance N1 was associated with the ERNs from both versions of the flanker task, supporting the possibility of shared neural processes. Replication of this association across two small populations across the adult lifespan provides strong preliminary support, but still requires replication in larger samples. While the majority of variance was shared across the three tasks, it is unclear whether the variance unique to the flanker tasks is task specific or related to a difference from the neural processes contributing to the balance N1. Important next steps will be to assess psychometric properties of the balance N1 in more rigorous experimental designs, and to determine whether the variance shared between the balance N1 and the ERN reflects the group and individual differences of interest to research in development and psychopathology. Further, if the balance N1 and ERN arise from shared underlying neural processes, further investigation may provide insight into links between balance and anxiety disorders.

To our knowledge, this is the first study comparing individual differences in the amplitude of the ERN between hand and foot response modalities. Internal consistency measures for the ERN were above 0.80 at most sites for both groups, indicating good reliability, consistent with previous reports (Riesel et al., 2013). Prior work has shown that ERN localization does not differ between hand and foot response modalities in young adults (Holroyd et al., 1998), and we now demonstrate that individual differences in ERN amplitudes are associated between these response modalities across the adult lifespan. This establishes a basis of comparison for similarity of ERNs across two objectively similar tasks, which we expected to be more similar to one another than to the balance N1. We did not expect the groups to differ in the site of maximal association between responses, but the ERNs were maximal at Fz with the exception of the ERN-hand in the older adults, which appeared to be larger at central sites. Although this seems odd, it is not unprecedented, as one study demonstrated that the scalp distribution of ERN amplitude association differs across pairings between Go/NoGo, Stroop, and flanker tasks (Riesel et al., 2013). Our data also replicate prior work demonstrating that the ERN amplitude is smaller in older compared to younger adults (Beste et al., 2009b; Nieuwenhuis et al., 2002).

The present studies demonstrate that the balance N1 is associated with the ERN in community samples of young and older adults. Although weaker than the association between ERNs, the present findings replicated a large effect size of the correlation between the ERN and the balance N1 across two groups of adults, supporting the possibility that these potentials arise from shared neural processes. Although one principal component captured most of the variance across the potentials, it remains to be tested whether this variance reflects the information that the ERN provides with respect to development (Tamnes et al., 2013) and psychopathology (Moser et al., 2013; Olvet & Hajcak, 2008; Seer et al., 2016). It is unclear whether differences in the tasks or in the underlying neural processes explain the ERN variance that was not shared with the balance N1. Although one study differentially localized the ERN to the anterior cingulate cortex and the balance N1 to the supplementary motor area in the same individuals (Marlin et al., 2014), it is possible that the nature of the stimulus determines the relative recruitment of these reciprocally connected cortical areas, similar to how the stimulus content determines the relative recruitment of the reciprocally connected cognitive and affective divisions within the anterior cingulate cortex (Bush, Luu, & Posner, 2000). If the balance N1 and the ERN arise from overlapping neural circuits, their relationship may provide insight into comorbidities between balance and anxiety disorders (Balaban, 2002; Balaban & Thayer, 2001; Bolmont, Gangloff, Vouriot, & Perrin, 2002; Jacob et al., 1997; Yardley & Redfern, 2001) and treatment, such as balance training that alleviates anxiety in young children (Bart et al., 2009) and the benefit of psychotherapy to balance disorders (Schmid, Henningsen, Dieterich, Sattel, & Lahmann, 2011; Yardley & Redfern, 2001).

There are some important limitations to consider. While the large effect size provides promising preliminary support of our hypothesis, it will be necessary to confirm these findings in a larger sample. The ERN was not the primary focus of these studies (Payne et al., 2022; Payne et al., 2021; Payne & Ting, 2020a; Payne & Ting, 2020c), and was always collected at the end of the session, after the physically active balance task. Although acute exercise does not necessarily influence the ERN (Themanson & Hillman, 2006), it is possible that the fixed task order had some effect. Using the same perturbation series across populations would have enabled more comparisons, but the older adults received much easier perturbations as a control population being compared against Parkinson's disease in another study (Payne et al., 2022). Although the excellent internal consistency reliability of the balance N1 suggests that a reliable estimate could be obtained using fewer trials, the possibility for habituation across initial trials should be carefully considered, especially where differences in habituation could present an additional source of individual differences (Payne et al., 2019a). While the even-odd method of splitting the data would balance any potential effect of initial habituation, the split-half reliability of the balance N1 was similar when splitting instead between the first and second half of trials, but this may not be the case when a non-randomized perturbation series is used (Quintern, Berger, & Dietz, 1985). Finally, although perturbations applied at the feet do not move the head during the balance N1, we strongly recommend the use of active electrodes and measurement of head acceleration, especially in more accessible methods of perturbing the trunk (Adkin et al., 2006; Mochizuki et al., 2010), which may accelerate the head at shorter latencies.

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