

# Distinct Cortical Correlates of Perception and Motor Function in Balance Control

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Fluctuations in brain activity alter how we perceive our body and generate movements but have not been investigated in functional whole-body behaviors. During reactive balance, we recently showed that evoked brain activity is associated with the balance ability in young individuals. Furthermore, in PD, impaired whole-body motion perception in reactive balance is associated with impaired balance. Here, we investigated the brain activity during the whole-body motion perception in reactive balance in young adults (9 female, 10 male). We hypothesized that both ongoing and evoked cortical activity influences the efficiency of information processing for successful perception and movement during whole-body behaviors. We characterized two cortical signals using electroencephalography localized to the SMA: (1) the “N1,” a perturbation-evoked potential that decreases in amplitude with expectancy and is larger in individuals with lower balance function, and (2) preperturbation  $\beta$  power, a transient rhythm that favors maintenance of the current sensorimotor state and is inversely associated with tactile perception. In a two-alternative forced choice task, participants judged whether pairs of backward support surface perturbations during standing were in the “same” or “different” direction. As expected, lower whole-body perception was associated with lower balance ability. Within a perturbation pair, N1 attenuation was larger on correctly perceived trials and associated with better balance, but not perception. In contrast, preperturbation  $\beta$  power was higher on incorrectly perceived trials and associated with poorer perception, but not balance. Together, ongoing and evoked cortical activity have unique roles in information processing that give rise to distinct associations with perceptual and balance ability.

**Key words:** balance;  $\beta$  rhythm; electroencephalography; N1; oscillations; perception

## Significance Statement

Fluctuations in the ongoing and evoked brain activity with identical sensory stimuli can give rise to different perceptual and motor outcomes. Such dynamic information processing is necessary for successful sensorimotor control in nonmobile tasks, but has not been investigated in perception and movement in functional whole-body behaviors. Here we show that perception and balance have distinct neural correlates; preperturbation activity was associated with better perception, whereas perturbation-evoked activity was associated with better balance. Our results support the hypothesis that both ongoing and evoked cortical activity during functional whole-body tasks contributes to successful perception and movement.

## Introduction

Ongoing and evoked cortical activity modulates perception during simple unimodal sensory detection tasks (Jones et al., 2010; Shin et al., 2017) and discrete upper limb movements (Little et al., 2019; Hussain et al., 2022). How cortical activity modulates complex multisensory processes required for whole-body sensorimotor control is unclear. When balance is perturbed, visual, somatosensory, and vestibular inputs are integrated to generate balance-correcting muscle activity (Horak, 2006; Welch and

Ting, 2008), which occurs automatically without conscious awareness. Sensory integration processes also give rise to conscious perception of the direction of whole-body motion, which varies across individuals (Puntkattalee et al., 2016) and could contribute to sensorimotor impairments in neurologic conditions (Halperin et al., 2020). Specifically, in PD, individuals with worse whole-body motion perception also had worse clinical balance function (Bong et al., 2020). Despite behavioral links between perception and motor abilities (Ostry et al., 2010;

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Edwards et al., 2019), their cortical mechanisms have traditionally been examined independently. When a tactile stimulus is applied to the fingertip in a seated position, variations in ongoing cortical activity prior to the stimulus influence detection accuracy (Jones et al., 2010). In reactive balance, perturbation-evoked activity during balance recovery reflects individual differences in balance ability (Ghosh et al., 2020; Payne and Ting, 2020a). However, the role of ongoing versus evoked cortical activity during the perception of reactive balance is unknown.

Assessing cortical activity in reactive balance offers a model to examine relationships between perception, movement, and brain activity in a functional whole-body context. Prior to conscious perception of whole-body motion, there is a robust negative event-related potential (N1) 100–200 ms postperturbation localized to the SMA (Marlin et al., 2014; Mierau et al., 2015; Solis-Escalante et al., 2020). Although the SMA is traditionally thought to contribute to the balance through error assessment and motor planning (Tanji, 1994; Nachev et al., 2008; Solis-Escalante et al., 2020), it also receives sensory inputs (Jürgens, 1984; Wiesendanger et al., 1985) and therefore may contribute to perception. N1 responses decrease with prior sensory stimulation (Staines et al., 2001), experience (Mierau et al., 2015; Payne et al., 2019a), and predictability (Adkin et al., 2006). Thus, N1 modulation may reflect a mechanism of dynamic information processing for perception and movement.

Fluctuations in prestimulus cortical activity modulate perception and movement in nonmobile settings (Jones et al., 2010; Shin et al., 2017; Little et al., 2019; Hussain et al., 2022), but have not been investigated in whole-body behaviors.  $\beta$  power is thought to support the maintenance of the “status quo” (Engel and Fries, 2010). In the motor domain,  $\beta$  power is higher at rest and decreases prior to movement, presumably to release the current sensorimotor state and prepare the system for upcoming sensorimotor processing (Barone and Rossiter, 2021). In the perceptual domain, higher  $\beta$  power is associated with lower tactile detection rates (Jones et al., 2010). Since higher  $\beta$  power favors maintenance of the current state, lower  $\beta$  power could enhance the system’s ability to process upcoming sensory signals to enhance perception and movement.

Here we hypothesized that ongoing and evoked cortical activity influences the information processing necessary for successful perception and movement. We characterized cortical activity localized to the SMA during directional perception of a whole-body motion as a function of perceptual accuracy and individual differences in the ability. Participants judged whether pairs of standing balance perturbations were in the “same” or “different” direction. We tested whether N1 modulation within a pair would be larger, reflecting greater anticipation of expected sensory inputs, for trials that are correctly perceived and in individuals with better balance ability. We further tested whether prestimulus  $\beta$  power would be lower, reflecting more efficient sensory processing, for correctly perceived trials and in individuals with better perceptual ability. Our findings reveal that perception and balance have distinct neural mechanisms. Larger N1 modulation was associated with better balance, whereas lower pre-perturbation  $\beta$  power was associated with better perception.

## Materials and Methods

**Participants.** Nineteen neurotypical young adults ( $24 \pm 5$  years, nine female) participated in a single experimental testing session. The sample size was selected based on prior work demonstrating the task-specific differences in cortical activity during perception (Jones et al., 2010; Shin et al., 2017) and reactive balance (Solis-Escalante et al., 2020;

Payne and Ting, 2020b) with sample sizes between 11 and 20, along with prior work that found significant correlations with large effect sizes (Cohen’s  $F^2 > 0.35$ ) between cortical activity and individual balance ability with sample sizes between 14 and 20 participants (Ghosh et al., 2020; Payne and Ting, 2020a; Palmer et al., 2021; Payne et al., 2021). The experimental protocol was approved by the Emory University Institutional Review Board, and all participants gave written informed consent before entering the study.

**Whole-body motion perception.** Participants stood barefoot with their arms across their chest and feet hip-width apart on a moveable platform. Pieces of tape were added to the platform for consistent foot placement and monitored online by the experimenter. Participants wore an overhead harness for safety, stood with their eyes closed, and wore headphones playing white noise to eliminate visual and auditory feedback.

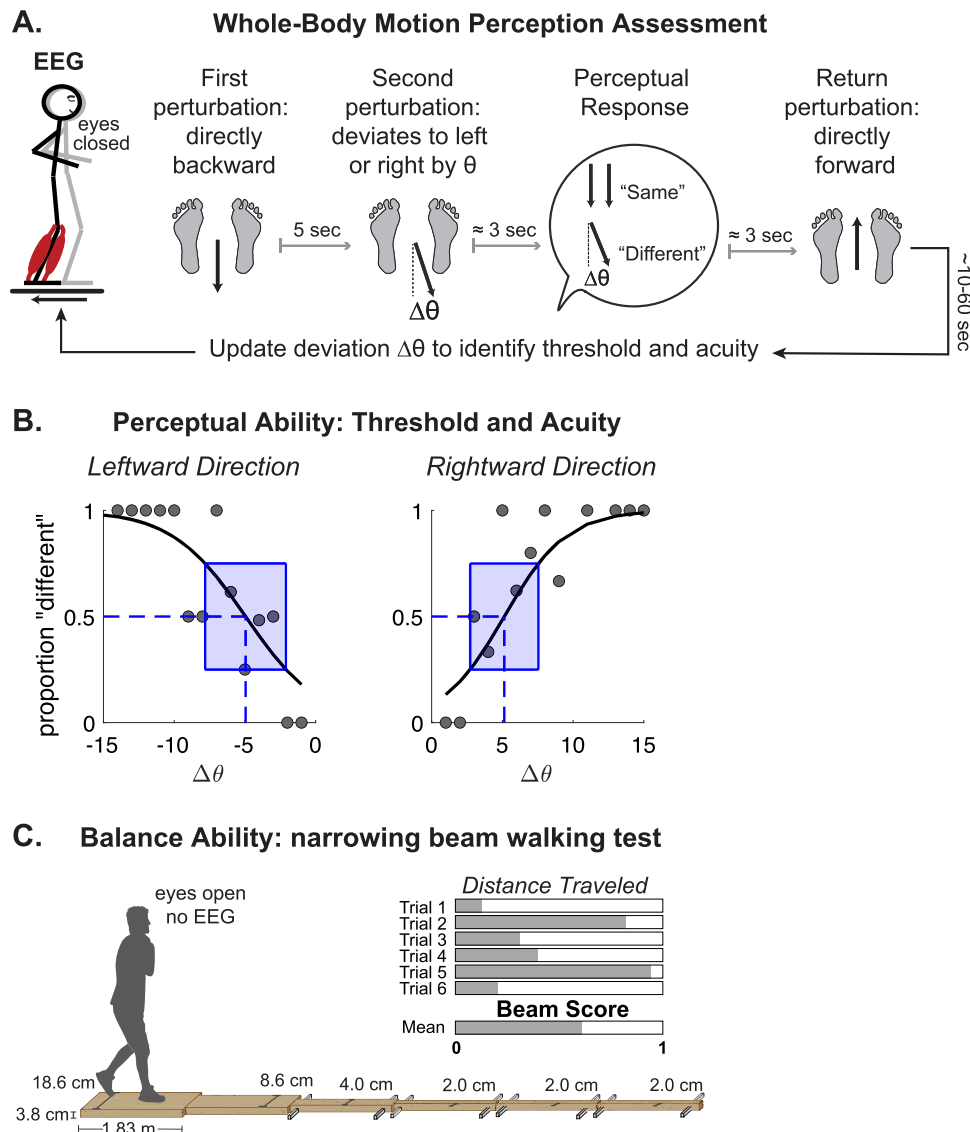
Participants underwent standing balance support surface translation perturbations (7.5 cm displacement, 15 cm/s velocity,  $0.1 \text{ m/s}^2$  peak acceleration) where they judged whether a pair of perturbations was in the same or different direction. The first perturbation of each pair was always straight backward. Five seconds after the first perturbation ended, a second perturbation was delivered backward with a lateral component ( $\Delta\theta$ ). Shortly after the end of the second perturbation ( $<3$  s), participants gave a verbal response of “same” or “different” (Fig. 1A; Bong et al., 2020; Puntkattalee et al., 2016). After each pair of perturbations, the platform return movement was always directly forward, that is,  $90^\circ$  to prevent participants from receiving any additional feedback regarding the direction of the perturbations. The timing of the first perturbation of each pair was unpredictable and varied between 10 and 60 s after the platform returned forward. The timing of the second perturbation of each pair was always 5 s after the first perturbation ended. Participants were not informed of any specific timing for the first or second perturbations of each pair, nor did they receive any external cues/preparatory signals.

There were two main blocks of perceptual testing. In the first testing block,  $\Delta\theta$  was adapted online using the  $\Psi$  (Psi) method through the Palamedes Toolbox in MATLAB (Prins and Kingdom, 2018). Unlike other adaptive algorithms, like parameter estimation by sequential testing (Taylor and Creelman, 1967) and staircase methods (Leek, 2001), the Psi method determines the perturbation angle ( $\Delta\theta$ ) after every trial, based upon the posterior distribution that contains the range of possible values of the slope and threshold parameters. Psi chooses angles that best predict the threshold and then chooses additional stimulus intensities well above and below the threshold to best predict the slope. The range of possible perturbation angles was linearly spaced from  $1$  to  $30^\circ$ , based on the thresholds obtained in our previously published work in young adults (Puntkattalee et al., 2016). A total of 60 pairs of perturbations were given, with right and left angles interleaved.

In the second testing block,  $\Delta\theta$  was individualized to each participant’s perceptual threshold for the right and left sides of platform movement. One hundred eight total pairs of perturbations were delivered. Two-thirds of these trials were administered at threshold (50% accuracy, 36 for each direction), and 1/3 were delivered at suprathreshold angles (75% and 95% accuracy, nine for each magnitude and direction). The order of the direction (left vs right) and angle ( $\Delta\theta$ ) was delivered in a pseudorandom order to minimize predictability. Participants were given seated rest breaks for  $\sim 3$ – $5$  min after every 20 trials, or upon request, to minimize fatigue and habituation.

Perceptual data from the psi block was fit with a psychometric function for the leftward and rightward directions of platform movement to characterize perceptual acuity and threshold. Acuity was defined as the interquartile range (Fig. 1B, dashed blue rectangle), and the threshold was defined as the angle at which perturbations were correctly discriminated as different on half of the trials (Fig. 1B, dotted pink line; Ostry et al., 2010; Wilson et al., 2010; Mirdamadi and Block, 2020).

**Balance ability.** Individual balance ability was assessed using a modified version of the narrowing beam walking test (Sawers and Hafner, 2018; Fig. 1C). To avoid a ceiling effect, the narrowing beam was extended to include two additional segments of the narrowest width



**Figure 1.** Perception and balance assessments. **A**, Whole-body motion perception protocol. EEG was continuously recorded during pairs of standing balance perturbations while participants had their arms across their chest and eyes closed. The second perturbation of each pair was delivered 5 s after the first perturbation ended and was identical in amplitude to the first but deviated at an angle. The angle of the second perturbation varied on a trial-by-trial basis and was unpredictable. After each pair, participants provided a verbal response of whether the perturbations were in the “same” or “different” directions. There was then a return perturbation that moved the platform directly forward, that is, 90°. The first perturbation of the subsequent pair began at an unpredictable timing, ~10–60 s after the return perturbation. **B**, Exemplar perceptual responses for a single participant for perturbation angles in the leftward and rightward direction of platform movement. Perceptual responses (gray dots) were fit with a logistic function to extract acuity (width of blue shaded rectangle) and threshold (blue vertical dashed line). Acuity defined as the difference between the 25th and 75th percentile. Threshold defined as the angle at which participants were equally likely to report “same” or “different.” **C**, The narrowing beam walking test was used as a metric of individual balance ability that required participants to walk one foot in front of the other with their arms across their chest and eyes open. No EEG was recorded during the task. The beam score was computed as the average proportional distance traveled across six trials.

(2 cm) for a total distance of 34 ft. Participants were instructed to walk one foot in front of the other with their arms across their chest wearing standardized footwear with their eyes open. There were no requirements for speed, and performance was assessed based on the average total distance traversed over six trials, normalized to the total beam length (Payne and Ting, 2020b). The distance for a trial was based on the toe of the foot that stepped off the beam or the distance of the front toe when their arms were uncrossed.

**EEG recording and analyses.** We recorded cortical activity during the whole-body motion perception task (sampling frequency, 1,000 Hz; impedance, <25 kOhm) using a 64-channel active electrode cap and active channel amplifier with a 24 bit A/D converter and an online 20 kHz anti-aliasing low-pass filter (Brain Products). Fz was the online reference electrode, and Fpz was the ground electrode.

EEG data were processed using the EEGLAB toolbox (Delorme and Makeig, 2004). Data were high-pass filtered (cutoff 0.5 Hz, finite impulse response, filter order of 3,300) and downsampled to 500 Hz. Bad channels were identified using the clean\_rawdata plugin (flat channel, >5 s; high-frequency noise, >4 SDs; or correlation with nearby channels, <0.6). Bad channels were confirmed with visual inspection and interpolated. The data were then rereferenced to an average reference across all channels. Sixty hertz line noise was removed with the Zapline-plus plugin (Klug and Kloosterman, 2022). The data were epoched –2 to 2 s around each perturbation and decomposed into maximally independent components (ICs) using the adaptive mixture independent component analysis (AMICA) algorithm (Palmer et al., 2008). ICs from AMICA were categorized using the ICLabel plugin, an automated algorithm that identifies nonbrain sources (e.g., eye, muscle, and cardiac activity) and brain sources, and confirmed with visual inspection (Pion-Tonachini et al., 2019).

Nonbrain sources were removed. Brain sources were mapped onto a standard Montreal Neurological Institute (MNI) template and estimated using the DIPFIT plugin in EEGLAB. Any ICs located outside of the brain or with high residual variance (RV; >15%) from the scalp projection of the best-fitting equivalent dipole were excluded prior to further analyses (Oostenveld and Oostendorp, 2002; Klug and Gramann, 2021). Brain ICs from each participant were clustered by a *K*-means clustering algorithm in the STUDY portion of EEGLAB using dipole location.

Analyses were performed on the cluster that gave rise to the largest cortical N1, which was localized to the SMA (Fig. 4A). If multiple ICs from a single participant clustered together, the IC with the largest percentage power accounted for (ppaf) between 100 and 200 postperturbation was used in the analyses (Fig. 4C, exemplar IC time course and associated ppaf).

To assess cortical responses postperturbation, we extracted single-trial N1 amplitudes that were baseline subtracted (−150 to −50 ms before perturbation onset) for each participant. The N1 was quantified as the largest negative peak 100–200 ms after perturbation onset.

To assess intrinsic fluctuations in the ongoing cortical activity prior to the perturbation, we extracted condition mean and single-trial preperturbation power spectra from −1,000 to 0 ms using Welch's method (nonoverlapping hamming windows, 500-window length) for each participant. The Fitting Oscillations and One-Over-F (FOOOF) toolbox (Donoghue et al., 2020) was used to decompose power spectra into aperiodic ( $1/f$ ) and periodic components (activity above  $1/f$ ) from 2 to 35 Hz using the following parameters: minimum peak height, 0.1; minimum peak width, 1; maximum number of peaks, 4; peak threshold, 2; and knee parameter, "fixed." Peak periodic  $\beta$  power was extracted from the fitted spectra from 13 to 30 Hz (Fig. 2B, pink vertical dashed line). If more than one peak was detected from 13 to 30 Hz, peak  $\beta$  power was averaged across the peaks. Since the width of peaks could also vary (Fig. 2B, left vs right column), we further extracted the area under the FOOOF spectra between 13 and 30 Hz (Fig. 2B, pink shaded area). Two representative example participants with contrasting perceptual thresholds had distinct differences in the magnitude of prestimulus  $\beta$  power (Fig. 2, left column vs right column). The individual with a lower perceptual threshold (Fig. 2, left column) had a lower prestimulus  $\beta$  power for the nonparameterized power spectra (Fig. 2A) and the parameterized periodic  $\beta$  power (Fig. 2B, pink dashed line and pink shaded area) compared with the individual with a higher perceptual threshold (Fig. 2, right column).

Since  $\beta$  power is known to have a timed and transient effect that emerges as bursts, we also extracted  $\beta$  events from single trials using the SpectralEvents toolbox. The toolbox defines events as local maxima in single-trial spectrograms that exceed a power threshold. We used the default parameters with a cutoff of six times the median power (Shin et al., 2017), to characterize  $\beta$  events from 13 to 30 Hz in the 1 s preperturbation window. For each trial, we characterized the number of  $\beta$  events,  $\beta$  event power,  $\beta$  event duration, and most recent event onset (i.e., closest to perturbation onset; Fig. 2C). The individual with lower perceptual threshold had fewer  $\beta$  events (white dots), lower event power, shorter event duration, and events further away from the perturbation onset (Fig. 2C, left column) in five representative trials. In contrast, the individual with a higher perceptual threshold had more frequent  $\beta$  events, higher event power, longer event duration, and events closer to perturbation onset (Fig. 2C, right column).

**Statistical analyses.** To test the interrelationships between perception, movement, and brain activity, we first examined the associations between whole-body motion perception and balance ability. We tested whether perceptual ability differed between the left and right directions of the platform movement using the paired sample *t* tests. We then tested the associations between whole-body motion perceptual ability and balance ability using independent correlations. For both *t* tests and correlations, analyses were performed separately for acuity and threshold.

To examine how evoked versus ongoing cortical activity varies within individuals, we ran separate linear mixed-effect models on N1 amplitude and prestimulus  $\beta$  power using predictor variables of perturbation order

and accuracy using the lmerTest package in R using the following formula:

$$\text{Cortical activity} = \beta_0 + \beta_1 \cdot \text{Perturbation order} + \beta_2 \cdot \text{Accuracy} + \beta_3 \cdot \text{Perturbation order} \cdot \text{Accuracy} + \varepsilon \quad (1)$$

Perturbation order and accuracy served as fixed effects, with reference levels of first (vs second) and correct (vs incorrect). Correct trials were those that were reported to be "different." Participants served as a random effect. To examine whether cortical activity changed over time with repeated trials, we also ran analyses on single-trial EEG data using the above model with the addition of the trial number as a categorical variable.

To examine whether evoked versus ongoing cortical activity reflects individual differences in perception and balance, we first ran separate independent correlations between N1 modulation ( $\Delta N1 = N1$  amplitude second perturbation, first perturbation) and prestimulus  $\beta$  power with ability (balance, acuity, threshold). We also performed multiple regression to evaluate balance, acuity, and threshold as predictors of  $\Delta N1$  and prestimulus  $\beta$  power.

To confirm the role of oscillatory  $\beta$  activity in perception and balance rather than broadband  $1/f$  activity, we ran parallel analyses (both within individuals and between individuals) on the aperiodic offset and aperiodic slope.

To examine the transient nature of  $\beta$  activity, we ran analyses as defined in Equation 1 with the addition of trial number, to determine which features of  $\beta$  events differed with the perceptual accuracy and perturbation order. Separate models were performed for the number of  $\beta$  events,  $\beta$  event power,  $\beta$  event duration, and most recent event onset. Finally, we compared  $\beta$  event features across individuals as a function of balance ability and perceptual ability, as described above.

Since the psi block was adaptive, the angles ranged from 0 to 30° depending on each individual's response and therefore variable across individuals. This block was used for quantifying each individual's perception (Fig. 1B, acuity and threshold). All statistical analyses on cortical activity were performed on the individualized block since this block had the largest number of trials that was at an equivalent level of perceptual challenge (i.e., threshold) across all participants. Two out of the 19 participants only had the psi block and were excluded from the cortical activity analyses.

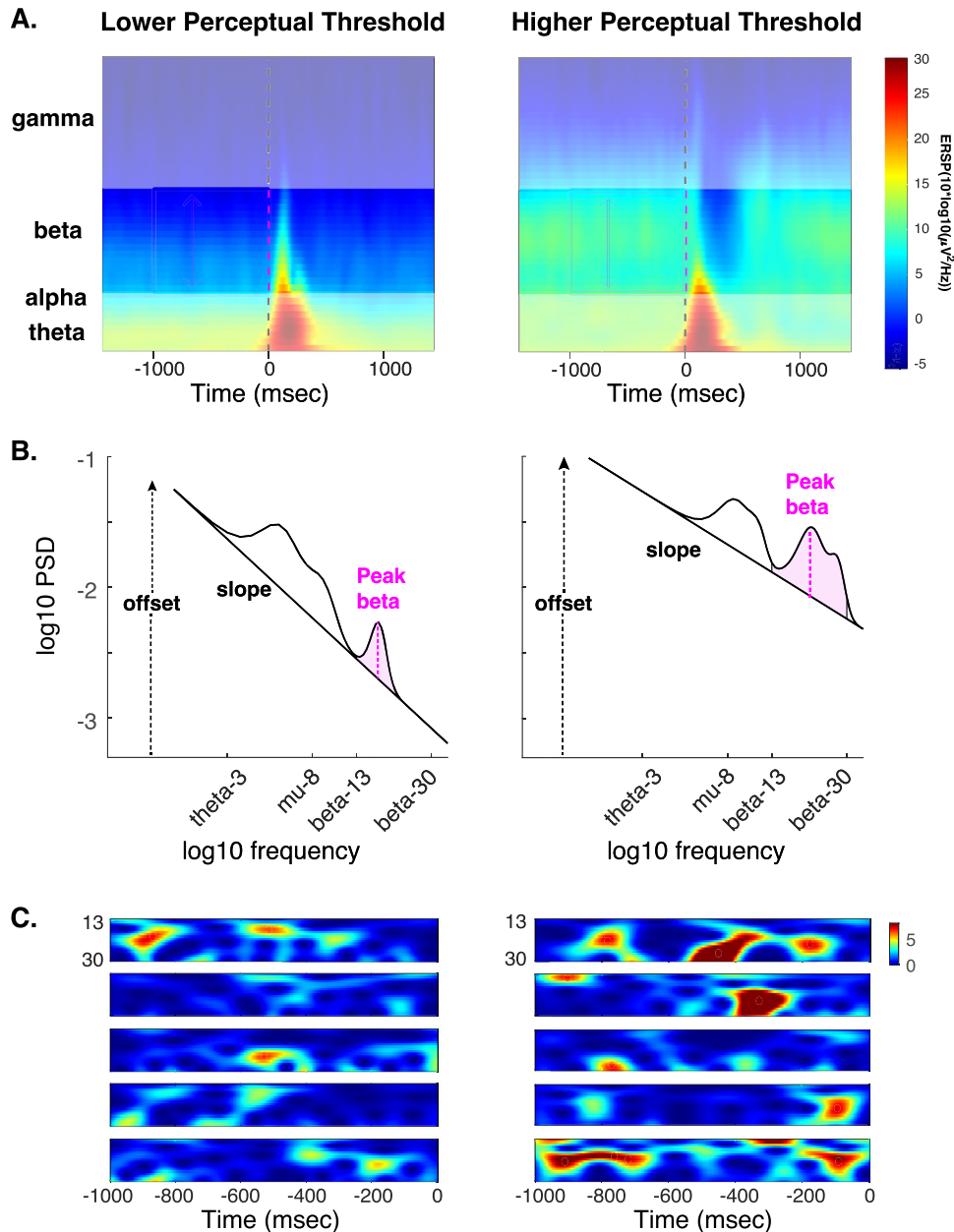
## Results

### Perception–balance associations

Perceptual acuity, the range of angles for which participants were correct in 25–75% of trials (Fig. 3A, width of shaded rectangles), ranged between 2.67 and 12.35° ( $5.32 \pm 2.59^\circ$ ), and perceptual threshold, the angle at which participants were correct 50% of the time (Fig. 3A, vertical dashed lines), ranged between 2.59 and 12.77° ( $7.9 \pm 2.73^\circ$ ). These values represent averages across left and right directions of platform movement, which were not significantly different [acuity, left,  $4.6 \pm 2^\circ$ ; right,  $6.2 \pm 4^\circ$  (mean  $\pm$  SD);  $p = 0.11$ ; threshold, left,  $7.6 \pm 3^\circ$ ; right,  $8.2 \pm 3^\circ$ ;  $p = 0.43$ ].

Across individuals, threshold and acuity were not associated ( $r = 0.29$ ,  $p = 0.22$ ). While some individuals had a lower threshold (better) and higher acuity (better; Fig. 3A, turquoise trace), others had a higher threshold (worse) and higher acuity (better; Fig. 3A, red trace).

Individual variations in perceptual acuity but not threshold were associated with balance ability (normalized distance, range, 0.41–0.84;  $0.63 \pm 0.11$ ). As an example, an individual with a relatively lower (i.e., better) threshold but worse acuity had relatively a lower balance function (Fig. 3A, green trace). In contrast, an individual with a relatively higher (i.e., worse) threshold but better acuity had better balance function (Fig. 3A, red trace). Across individuals, worse whole-body motion perception acuity was associated with a lower balance ability (Fig. 3B,  $r = -0.69$ ,



**Figure 2.** Exemplar spectral data from two participants with different perceptual abilities. **A**, Time–frequency spectrograms pre- and postperturbation. The pink rectangle denotes  $\beta$  range (13–30 Hz) analyzed preperturbation (–1,000 to 0 ms). **B**, Log-transformed prestimulus (–1,000 to 0 ms) power spectral density parameterized into periodic and aperiodic components. Aperiodic power ( $1/f$  component that is linear with log transformation) described by the slope and offset. Periodic power represented by peaks above the aperiodic component.  $\beta$  power was described using peak power (pink dashed line) and AUC (pink shaded region) from 13 to 30 Hz in the 1,000 ms prior to the perturbation. An individual with a lower perceptual threshold (better ability) had a lower prestimulus  $\beta$  power (left column) compared with the individual with a higher perceptual threshold (right column). **C**,  $\beta$  event characteristics of five single trials in the 1,000 ms prior to the perturbation. An individual with a lower perceptual threshold (left column) had fewer  $\beta$  events (white dots), lower  $\beta$  event power, shorter  $\beta$  event duration, and events further from perturbation onset compared with the individual with a higher perceptual threshold (right column).

$p = 0.001$ ). While a similar direction of association was observed for perceptual threshold with balance ability, the correlation was not statistically significant (Fig. 3C,  $r = -0.39$ ,  $p = 0.102$ ).

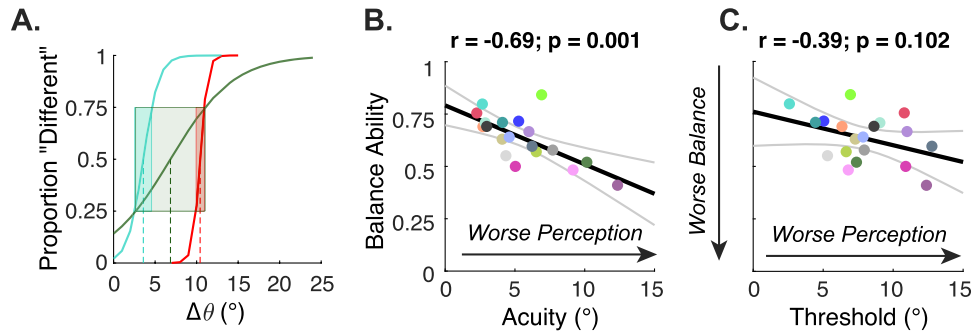
### Source localization

Consistent with prior studies (Marlin et al., 2014; Mierau et al., 2015; Solis-Escalante et al., 2020), the source that contributed the largest to the N1 was localized to the SMA (Fig. 4A, individual equivalent current dipoles denoted by blue circles). IC scalp maps were similar across participants and illustrate a midfrontal topography (Fig. 4B). The estimated location, RV, ppaf, and

the IC that gave rise to the largest N1 potential between 100 and 200 ms postperturbation (Fig. 4C, exemplar participant) for each participant are shown in Table 1. One participant was excluded due to high electrode impedance from most sensors related to hairstyle.

### Task- and individual-specific perturbation-evoked N1 responses

N1 amplitude on a single perturbation was smaller on the second compared with the first and decreased across trials for both correct (i.e., “different”) and incorrect responses (i.e., “same”). Mean



**Figure 3.** Individual differences in perception and balance ability. **A**, Exemplar psychometric curves during whole-body motion perception task for three participants with varying acuity (shaded rectangles) and threshold (vertical dashed lines). Two participants (turquoise, red) with relatively better acuity (narrower rectangles, smaller interquartile ranges) despite contrasting thresholds (turquoise, better; red, worse) had better balance. The third exemplar participant (green) had a better threshold but worse acuity and had relatively worse balance. **B**, Lower perceptual acuity was associated with lower balance ability. **C**, Perceptual threshold was not associated with balance ability.

**Table 1. Characteristics of primary source contributing to the N1 potential for each participant**

Participant	x	y	z	Ppaf	RV
1	-6.21	-11.64	71.97	96.66	2.35
2	10.06	-8.69	67.68	85.93	4.92
3	-0.42	-13.69	63.13	80.15	2.49
4	4.16	1.42	54.19	85.97	2.85
5	2.64	-9.44	61.52	65.81	4.28
6	-0.98	-19.1	57.47	87.85	1.35
7	-1.24	-8.15	72.1	79.27	3.97
8	-0.29	-25.18	55.93	79.16	2.46
9	3.31	8.8	52.48	74.11	1.46
10	0.29	-15.51	68.45	96.49	0.77
11	-5.99	-20.13	50.21	79.93	1.6
12	2.18	-9.27	57.93	92.48	1.52
13	-4.09	-20.95	73.22	87.57	1.43
14	2.26	-10.52	64.54	74.7	1.12
15	-5.57	-1.26	47.39	62.78	2.89
16	2.98	-13.05	48.85	93.71	2.75
mean	0.19	-11.02	60.44	82.66	2.39

MNI coordinates of the IC that contributed the largest to the N1 potential 100–200 ms postperturbation. Ppaf – percentage power accounted for. RV – residual variance.

N1 amplitude was smaller on the second perturbation compared with the first [ $b_{\text{Perturbation Order}} = -1.99 \mu\text{V}$ , 95% CI (-2.32, -1.65),  $t_{45} = -11.95$ ,  $p < 0.001$ ; Fig. 5, pink vs black bars]. The N1 amplitude on either the first or the second perturbation was similar regardless of perceptual accuracy ( $p = 0.28$ ; Fig. 5A vs B). These results were further substantiated using single-trial N1 amplitudes; there was a significant decrease in N1 amplitude within a perturbation pair [ $b_{\text{Perturbation Order}} = -2.04 \mu\text{V}$ , 95% CI (-2.24, -1.84),  $t_{2,948.02} = -20.11$ ,  $p < 0.001$ ]. N1 amplitude also decreased across trials [ $b_{\text{Trial Number}} = -0.01\%$ , 95% CI (-0.01, -0.01),  $t_{2,949.51} = -8.15$ ,  $p < 0.001$ ] regardless of perceptual accuracy [ $b_{\text{Accuracy}} = -0.18\%$ , 95% CI (-0.41, 0.05),  $t_{2,948.30} = 1.56$ ,  $p = 0.12$ ]. To confirm that the N1 reduction across trials was similar regardless of perceptual accuracy, we ran a separate model that included an interaction term for trial number and accuracy and found no significant interaction [ $b_{\text{Accuracy} \times \text{Trial Number}} = 0.00\%$ , 95% CI (-0.00, 0.01),  $t_{2,947.26} = 0.98$ ,  $p = 0.328$ ].

Since N1 decreased within a perturbation pair, we ran a parallel analysis on single-trial N1 modulation ( $\Delta\text{N1} = \text{N1 amplitude on second} - \text{first perturbation}$ ). N1 modulation within a perturbation pair was larger on correctly perceived trials versus incorrectly perceived trials [Fig. 6A,  $b_{\text{Accuracy}} = 0.42\%$ , 95% CI (0.11, 0.72),  $t_{1,528.38} = 2.65$ ,  $p = 0.008$ ] and decreased with repeated trials

[ $b_{\text{Trial Number}} = -0.01\%$ , 95% CI (-0.01, -0.00),  $t_{1,534.81} = -2.21$ ,  $p = 0.028$ ].

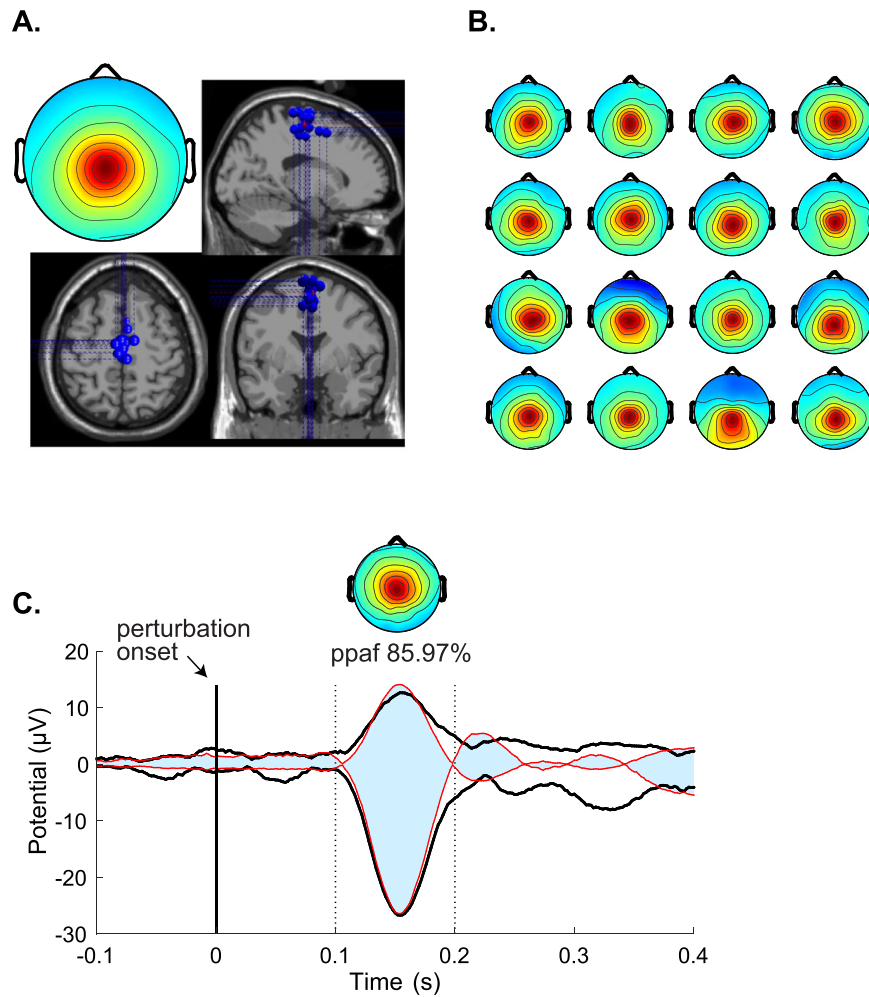
Across individuals, better balance ability was associated with larger N1 attenuation, but only for the correctly perceived perturbations (correct,  $r = -0.56$ ,  $p = 0.02$ , Fig. 6Bi; incorrect,  $r = -0.16$ ,  $p = 0.56$ , Fig. 6Bii). Neither perceptual threshold (Fig. 6Ci,ii, all  $p > 0.39$ ) nor acuity was associated with N1 attenuation, regardless of perceptual accuracy. The specificity of the associations between balance ability and not perceptual ability on N1 modulation was confirmed with multiple regression, using predictors of balance, threshold, acuity, and accuracy. The multiple regression revealed an interaction between balance and accuracy on N1 modulation [ $b_{\text{Balance} \times \text{Accuracy}} = 5.09\%$ , 95% CI (1.27, 8.92),  $t_{12} = -2.90$ ,  $p = 0.013$ ]. The other predictors of acuity, threshold, and any interaction with accuracy on  $\Delta\text{N1}$  were not significant (all  $p > 0.08$ ). N1 associations with balance ability were specific to N1 attenuation within a pair; there were no associations between N1 amplitude evoked by either the first or second perturbation and ability (all  $p > 0.19$ ).

#### Task- and individual-specific pre-perturbation cortical activity

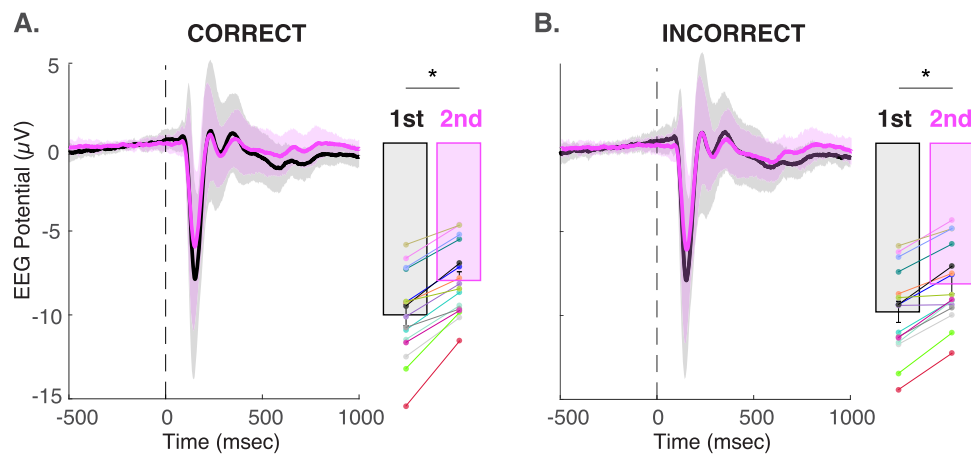
Preperturbation peak  $\beta$  power was higher when perception was incorrect compared with when perception was correct [ $b_{\text{Accuracy}} = 0.07\%$ , 95% CI (0.015, 0.125),  $t_{45} = 2.55$ ,  $p = 0.014$ ] but did not change within a perturbation pair [ $b_{\text{Perturbation Order}} = 0.02\%$ , 95% CI (-0.032, 0.078),  $t_{45} = 0.85$ ,  $p = 0.40$ ; Fig. 7A]. This pattern was also observed for  $\beta$  area under the curve [ $b_{\text{Accuracy}} = 0.81\%$ , 95% CI (0.12, 1.50),  $t_{45} = 2.36$ ,  $p = 0.023$ ;  $b_{\text{Perturbation Order}} = -0.14\%$ , 95% CI (-0.83, 0.55),  $t_{45} = -0.42$ ,  $p = 0.68$ ; Fig. 7B].

Single-trial preperturbation  $\beta$  power analyses revealed that  $\beta$  power was higher for incorrectly perceived trials compared with correctly perceived trials, but only for the first perturbation [ $b_{\text{Accuracy} \times \text{Perturbation Order}} = -0.08\%$ , 95% CI (-0.13, -0.02),  $t_{2,879.72} = -2.69$ ,  $p = 0.007$ ;  $b_{\text{Accuracy}} = 0.05\%$ , 95% CI (0.01 to 0.09),  $t_{2,886.31} = 2.32$ ,  $p = 0.021$ ]. Peak  $\beta$  power was not systematically modulated with repeated trials ( $p = 0.71$ ). A similar pattern was observed for single-trial  $\beta$  area under curve (AUC), with higher  $\beta$  power on the first compared with the second perturbation but only for incorrect trials [ $b_{\text{Accuracy} \times \text{Perturbation Order}} = 1.07\%$ , 95% CI (-2.11, -0.03),  $t_{2,878.32} = -2.03$ ,  $p = 0.043$ ], with no systematic change in power across repeated trials ( $p = 0.62$ ).

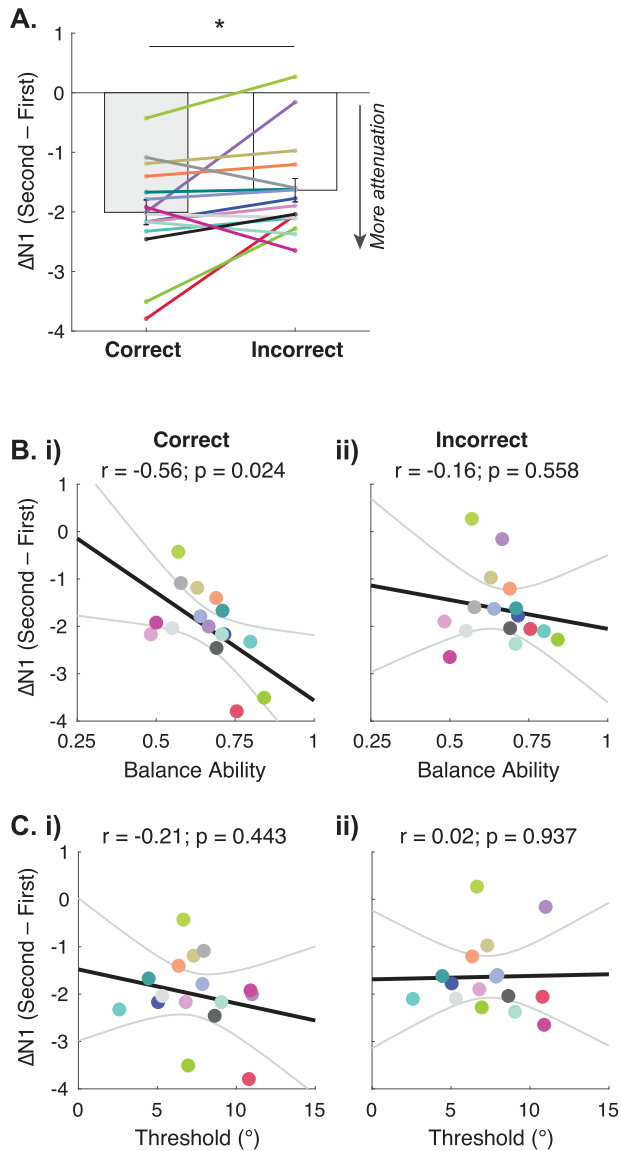
There was no effect of perceptual accuracy on preperturbation aperiodic parameters (exponent, offset). Both the exponent and offset showed a small but significant increase within a perturbation pair [exponent,  $b_{\text{Perturbation Order}} = 0.05\%$ , 95% CI: (0.01, 0.10),  $t_{45} = 2.42$ ,  $p = 0.020$ ; offset,  $b_{\text{Perturbation Order}} = 0.07\%$ , 95% CI



**Figure 4.** Source localization of N1 responses. **A**, Group scalp topography and localization. Centroid of individual ICs (blue dots) localized to right BA6 MNI coordinates ( $X=0$ ,  $Y=-11$ ,  $Z=60$ ). **B**, Scalp maps for each participant showing the topographic distribution of the IC with the largest contribution to the N1 projected across all channels. The red color indicates higher activity over midcentral electrodes. **C**, IC time series for exemplar subject, with the N1 contributing to 86% power accounted for 100–200 ms post-perturbation (dashed vertical lines). The thick black lines denote the data envelope—the maximum and minimum activation of all brain ICs projected across all electrodes. The red line denotes the envelope for IC that contributed the largest to the N1 response. The blue shaded area denotes the proportion of signal from a single IC that contributes to the overall signal across all electrodes (ppaf).



**Figure 5.** Perturbation-evoked potentials and N1 amplitudes extracted from SMA source across perturbation conditions. The thick solid line and shaded region of the ERP trace denote the mean and standard deviation, respectively. Bars denote the mean N1 amplitude. Error bars indicate SEM. N1 amplitude decreased on the second perturbation relative to the first perturbation for both correctly perceived trials (**A**) and incorrectly perceived trials (**B**). \* denotes effect of perturbation order:  $p < 0.001$ .



**Figure 6.** N1 modulation across individuals within a pair of perturbations versus ability. **A**, N1 attenuation (more negative  $\Delta N1$ ) was larger for correctly perceived trials compared with incorrectly perceived trials. \* denotes  $p = 0.008$ . Error bars indicate SEM. **B**, Larger N1 attenuation was associated with better balance ability for correctly perceived trials (*i*) but not incorrectly perceived trials (*ii*). **C**, There were no associations between N1 attenuation and perceptual threshold for either correctly perceived trials (*i*) or incorrectly perceived trials (*ii*).

(0.01, 0.12),  $t_{45} = 2.56$ ,  $p = 0.014$ ]. However, single-trial analyses of these parameters revealed no significant effects or interactions.

Across individuals, lower perceptual thresholds (i.e., better ability) were associated with lower prestimulus  $\beta$  AUC, regardless of perceptual accuracy (Fig. 8*Bi,ii*; correct,  $r = 0.76$ ,  $p = 0.001$ ; incorrect,  $r = 0.73$ ,  $p = 0.001$ ). Neither perceptual acuity nor balance ability (Fig. 8*Ai,ii*) was associated with prestimulus  $\beta$  power. These results were confirmed with multiple regression using predictors of balance, threshold, acuity, and accuracy, on prestimulus  $\beta$  power. The multiple regression revealed that only the threshold predicted prestimulus  $\beta$  power [ $b_{\text{Threshold}} = 0.92\%$ , 95% CI (0.45, 1.39),  $t_{13.6} = 4.18$ ,  $p = 0.001$ ]. The other predictors of acuity, balance, and any interaction with accuracy were not significant (all  $p > 0.16$ ).

There were no associations between aperiodic parameters and acuity, threshold, or balance (all  $p > 0.11$  for independent

correlations), supporting the specific role of periodic oscillatory  $\beta$  power in explaining individual differences in threshold rather than a combination of oscillations and broadband power.

### $\beta$ event characteristics within and between individuals

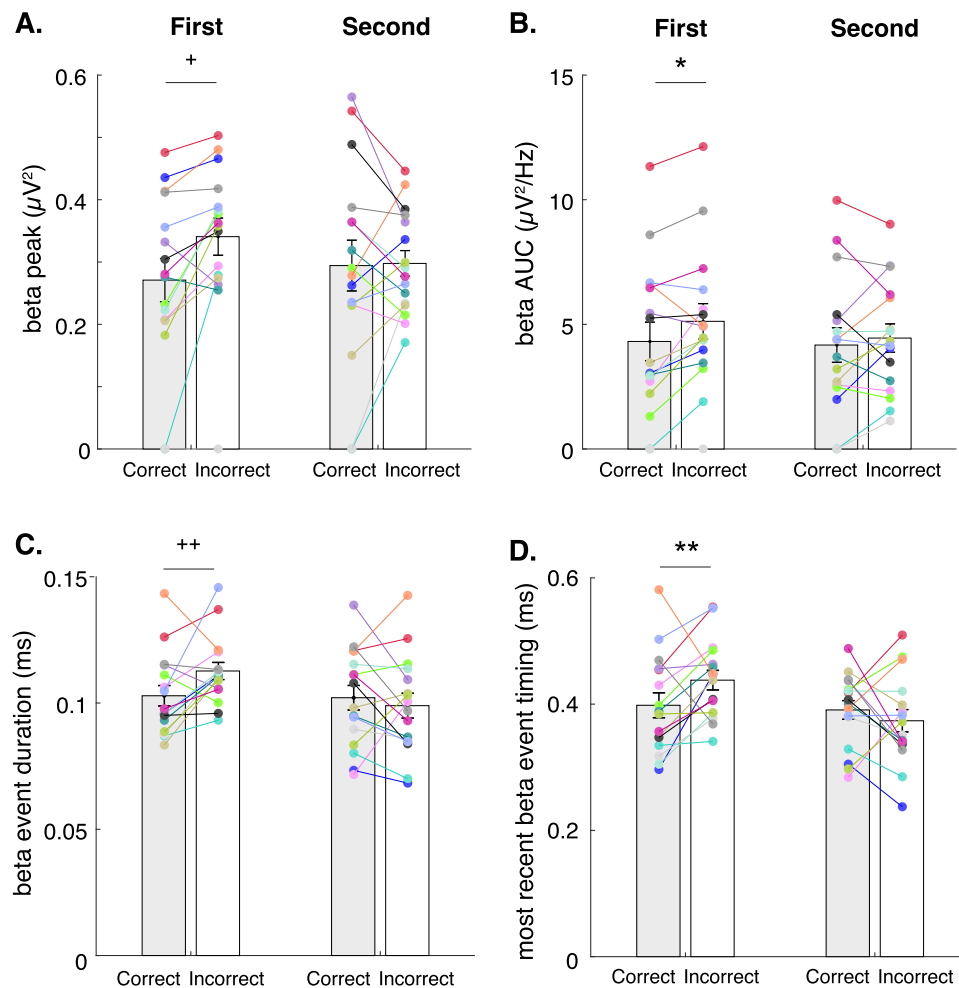
Higher periodic  $\beta$  power prior to perturbations that were incorrectly perceived could reflect a number of different  $\beta$  event features, such as longer burst duration, more frequent events, and/or higher power of individual events. The number of  $\beta$  events prior to the first perturbation tended to be higher for incorrectly perceived trials but did not reach statistical significance [ $b_{\text{Accuracy}} = 0.14\%$ , 95% CI (-0.01 to 0.29),  $t_{3,098.33} = 1.84$ ,  $p = 0.066$ ].  $\beta$  event power prior to either the first or second perturbation was similar regardless of perceptual accuracy (all  $p > 0.094$ ).  $\beta$  events prior to the first perturbation were longer for incorrectly perceived trials compared with correctly perceived trials [ $b_{\text{Accuracy}} = 0.01\%$ , 95% CI (0.00 to 0.02),  $t_{3,100.16} = 2.06$ ,  $p = 0.039$ ]. In contrast,  $\beta$  event duration prior to the second perturbation tended to be similar regardless of accuracy [ $b_{\text{Accuracy} \times \text{Perturbation Order}} = -0.01\%$ , 95% CI (-0.02 to 0.00),  $t_{3,090.11} = -1.79$ ,  $p = 0.074$ ; Fig. 7*C*].  $\beta$  events prior to the first perturbation occurred closer to perturbation onset for incorrectly perceived trials compared with correctly perceived trials [ $b_{\text{Accuracy} \times \text{Perturbation Order}} = -0.06\%$ , 95% CI (-0.11 to 0.01),  $t_{3,090.20} = -2.28$ ,  $p = 0.022$ ;  $b_{\text{Accuracy}} = 0.04\%$ , 95% CI (0.01 to 0.08),  $t_{3,102.97} = 2.40$ ,  $p = 0.017$ ; Fig. 7*D*].

Based on  $\beta$  event duration and the most recent  $\beta$  event timing having the strongest effects of perceptual accuracy, we then ran correlational analyses and multiple regression to look at individual differences in perceptual and balance ability. Similar to our findings with periodic  $\beta$  power, we found that longer  $\beta$  events or more recent  $\beta$  events prior to correctly perceived trials were associated with a worse perceptual threshold (duration,  $r = 0.62$ ,  $p = 0.011$ ; timing,  $r = 0.53$ ,  $p = 0.035$ ). The associations between threshold and  $\beta$  events prior to incorrectly perceived trials followed a similar direction of association but did not reach statistical significance (duration,  $r = 0.46$ ,  $p = 0.071$ ; timing,  $r = 0.42$ ,  $p = 0.11$ ). Neither  $\beta$  duration nor the most recent event timing was associated with balance ability or acuity (all  $p > 0.43$ ). These results were confirmed with multiple regression using predictors of balance, threshold, acuity, and accuracy, on prestimulus  $\beta$  event features. The multiple regression revealed that only the threshold predicted prestimulus  $\beta$  duration [ $b_{\text{Threshold}} = 0.005\%$ , 95% CI (0.002, 0.008),  $t_{18.0} = 3.22$ ,  $p = 0.005$ ]. The other predictors of acuity, balance, and any interaction with accuracy were not significant (all  $p > 0.12$ ). A similar pattern was observed for the most recent event  $\beta$  timing, with the threshold being the only significant predictor of  $\beta$  [most recent event timing,  $b_{\text{Threshold}} = 0.012\%$ , 95% CI (0.00, 0.024),  $t_{20.7} = 2.09$ ,  $p = 0.049$ ]. The other predictors of acuity, balance, or their interactions with accuracy were not significant (all  $p > 0.39$ ).

## Discussion

Here we show, for the first time, the relationships between brain activity, perception, and movement that contribute to functional balance control. We identified two distinct cortical activity metrics that vary across trials with perceptual accuracy and are uniquely associated with individual differences in balance and perceptual ability. First, we propose that attenuation of perturbation-evoked N1 potentials reflects dynamic information processing important for balance control. N1 attenuation within a pair of perturbations during a whole-body perceptual task was larger for correctly perceived trials and across individuals was





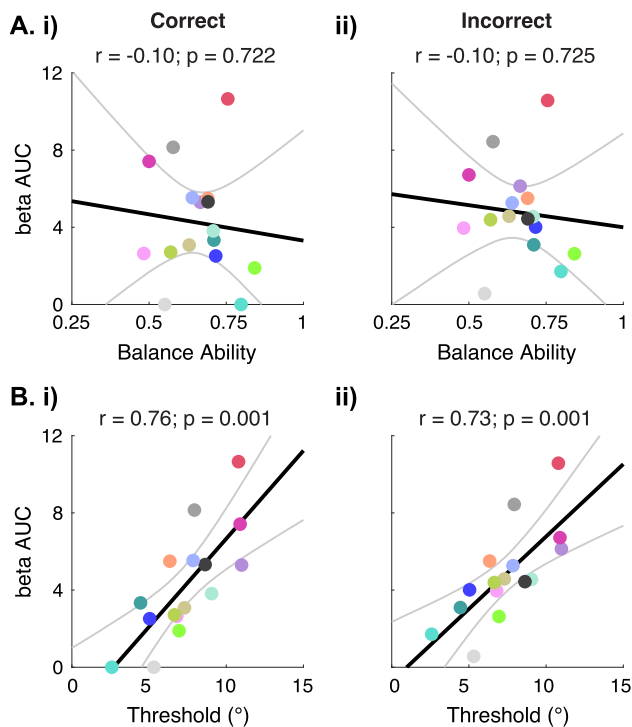
**Figure 7.** Prestimulus  $\beta$  activity across perturbation conditions and single trials. Prestimulus  $\beta$  power was higher when perception was incorrect compared with correct, but only on the first perturbation of the pair. There were no differences in  $\beta$  power with accuracy for the second perturbations of the pair. There was a similar pattern for peak  $\beta$  power (**A**) and  $\beta$  AUC (**B**). Across single trials,  $\beta$  events prior to the first perturbation were longer in duration (**C**) and occurred closer to perturbation onset (**D**) for incorrectly perceived trials compared with correctly perceived trials. + denotes  $p = 0.014$ ; \* denotes  $p = 0.023$ ; ++ denotes  $p = 0.039$ . \*\* denotes  $p = 0.017$ . Error bars indicate SEM.

associated with better balance ability. This attenuated brain activity may reflect the ability of the nervous system to modulate its response to predictable future events. Second, since  $\beta$  power reflects the maintenance of the status quo (Engel and Fries, 2010), our findings suggest that higher  $\beta$  power reduces the system's sensitivity to processing sensory inputs.  $\beta$  power was higher on incorrectly perceived trials and across individuals was associated with higher (i.e., worse) perceptual thresholds.  $\beta$  power may thus reflect inhibitory mechanisms that affect sensory information processing necessary for perception. These brain–behavior linkages provide mechanistic insight underlying individual differences in sensorimotor function that may be important in health and disease.

### Perceptual–balance interactions

The positive association between directional perception and balance ability highlights the important role of multisensory integration processes in maintaining balance. A similar relationship was found between impaired directional perception and clinical balance function using the miniBEST in PD, but not healthy older adults, potentially due to a ceiling effect of the miniBEST in older adults (Bong et al., 2020). Here, we used the narrowing beam walking test as a more sensitive balance assessment tool (Sawers and Hafner, 2018), revealing associations between

perceptual acuity and balance ability in young adults. Surprisingly, there was no association between perceptual threshold and balance ability, highlighting the importance of characterizing both acuity and threshold of psychometric functions. Perceptual acuity and threshold are not necessarily dependent (Hoseini et al., 2015); one individual can be highly sensitive with a large threshold, while another can be highly sensitive with a small threshold. We speculate that higher acuity reflects a higher certainty of perception for successful balance. The association between balance and perceptual acuity but not threshold could reflect the complexity of the narrowing beam task that requires dynamic fine-tuning of muscle activity. Efficient postural adjustments using subtle changes in sensory input on the beam may be more representative of individuals with high perceptual acuity, regardless of their overall threshold. Because a discrimination task was used, we cannot rule out contributions of working memory in perception. Further, other factors besides directional discrimination, such as speed detection, may be important for understanding the complexity of perceptual–balance interactions. Despite these limitations, our findings on perceptual–balance interactions in PD and young adults set the groundwork for future research to clarify the causal contributions of perception on balance control.



**Figure 8.** Prestimulus  $\beta$  power across individuals versus ability. **A.** Prestimulus  $\beta$  power was not associated with balance ability for either correctly perceived trials (*i*) or incorrectly perceived trials (*ii*). **(B)** Individuals with higher prestimulus  $\beta$  power had higher (i.e., worse) thresholds for both correctly perceived trials (*i*) and incorrectly perceived trials (*ii*).

### N1 attenuation is important for balance control

The N1 was localized to SMA, an area that integrates sensory, motor, and cognitive information to evaluate and respond to errors (Tanji, 1994; Nachev et al., 2008; Bonini et al., 2014). Evaluating an error signal involves comparing the expected versus actual sensory feedback, which presumably could affect perception. However, we observed similar N1 amplitudes regardless of the perceptual response, suggesting that the N1 is more reflective of initial sensory encoding that is not integrated into a conscious percept. Decreases in N1 amplitude across trials are consistent with prior literature suggesting that the N1 is influenced by perturbation predictability and experience (Adkin et al., 2006; Mierau et al., 2015; Payne et al., 2019a), potentially mediated by cognitive control (Payne et al., 2019b).

N1 attenuation within a perturbation pair may reflect the ability to dynamically respond to predictable sensory input that varies within and between individuals. Because the second perturbation in each pair occurred at predictable timing and magnitude, individuals could anticipate the second perturbation, resulting in smaller N1 amplitudes. Greater N1 attenuation for correctly perceived trials suggests better predictability of the expected postural state thereby enhancing the system's sensitivity to upcoming sensory inputs. The N1 attenuation observed here is similar to that in unimodal paired pulse paradigms where early cortical responses are smaller on the second stimulus relative to the first (Cromwell et al., 2008), thought to be mediated by sensory gating. Sensory gating occurs to prevent sensory overflow and optimize neural resources for processing novel inputs (Azim and Seki, 2019). Here, greater gating could serve to filter out irrelevant sensory information that increases the salience of the second perturbation for accurate perception. While prior studies have linked reduced sensory gating to reduced tactile

perception in aging (Cheng and Lin, 2013; Spooner et al., 2019) and neurological dysfunction (Arpin et al., 2017; Nguyen et al., 2020), this is the first study to demonstrate its functional relevance to trial-by-trial reductions in whole-body motion perception accuracy.

Between individuals, N1 attenuation within a pair may reflect dynamic information processing necessary for successful balance, since larger N1 attenuation was associated with better balance ability. Reduced N1 modulation may be inefficient for processing subtle changes in sensory input (Azim and Seki, 2019) in balance control. N1 modulation may reflect the modulation of motor or cognitive responses with changes in task demands or conditions or the “central set” necessary for successful balance (Horak et al., 1989). In older adults with and without PD, the inability to change sets has been linked to inflexible postural responses and balance impairments (Chong et al., 2000; Payne et al., 2021). Here, associations between balance ability and N1 modulation rather than absolute N1 amplitude suggest that it is the ability to change sets, that is, alter responses to predictable sensory input, rather than a single error signal that has functional relevance to balance. The lack of association with N1 modulation and perceptual ability further points to a distinction between initial sensory processing and higher-order processes for perception.

### $\beta$ oscillations play a distinct role in whole-body motion perception

Our data suggest that prestimulus  $\beta$  power sets the sensitivity of the perceptual system within and between individuals. We show that the inhibitory role of  $\beta$  processes in simple unimodal detection or single joint movements in a seated position (Jones et al., 2010; Little et al., 2019) is relevant during functional whole-body behaviors. Lower  $\beta$  power may represent more effective sensory processing, potentially by increasing the salience of somatosensory signals to discriminate the direction of the whole-body motion. Higher prestimulus  $\beta$  power for incorrectly perceived judgments is consistent with the role of  $\beta$ , maintaining the “status quo” (Engel and Fries, 2010), potentially decreasing the system's sensitivity to sensory input necessary to discriminate the whole-body motion.

Further support for the inhibitory influence of  $\beta$  power on perception comes from the finding that individuals with higher prestimulus  $\beta$  power had higher (i.e., worse) perceptual thresholds. If  $\beta$  power reflects inhibitory processing, higher prestimulus  $\beta$  power may favor the current sensorimotor state (Engel and Fries, 2010), potentially at the expense of processing new sensory information elicited by balance perturbations, resulting in higher thresholds. Since we parameterized power spectra into periodic and aperiodic components, these findings are unlikely to be driven by nonrhythmic activity. The specific role of  $\beta$  oscillations in perception was further substantiated by the findings that neither the aperiodic exponent nor offset correlated with perceptual ability.

The presence and timing of transient  $\beta$  events varied within and between individuals, potentially through the recruitment of inhibitory mechanisms that decreases sensory transmission. Similar to tactile perception (Shin et al., 2017),  $\beta$  events prior to perturbations were longer in duration and closer to the perturbation onset for incorrectly perceived trials compared with correctly perceived trials. These findings extend the temporal and functional specificity of  $\beta$  events known to govern trial-by-trial fluctuations in constrained tasks (Shin et al., 2017; Little et al., 2019) to functional whole-body behaviors.

The roles of ongoing versus evoked activity in perceptual threshold and balance ability, respectively, reflect different mechanisms by which the SMA processes information for perception and movement. The lack of associations between cortical activity and perceptual acuity suggests that acuity may be mediated by other sources important for balance such as anterior cingulate or parietal regions (Purohit and Bhatt, 2022). A logical next step is to manipulate cortical activity to determine their causal roles in functional balance control.

### Ongoing versus evoked cortical activity has distinct roles in perception and movement

Our findings extend the role of cortical activity in perception and movement, traditionally studied in isolation during simple tasks, to functional balance control that requires both perception and movement. The distinct associations between cortical activity and functional behaviors have important implications for understanding perceptual–motor interactions in people with impaired balance. Reduced sensory gating and elevated  $\beta$  power observed with aging, stroke, and PD may reflect different mechanisms of inefficient information processing necessary for perception and movement (Brown, 2003; Rossiter et al., 2014; Thibaut et al., 2017; Azim and Seki, 2019; Espenhahn et al., 2020). A better understanding of the brain activity during functional balance control may help dissociate balance and perceptual deficits and guide mechanistic-based rehabilitation interventions.

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