



## Directional acuity of whole-body perturbations during standing balance



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### ABSTRACT

The ability to perceive the direction of whole-body motion during standing may be critical to maintaining balance and preventing a fall. Our first goal was to quantify kinesthetic perception of whole-body motion by estimating directional acuity thresholds of support-surface perturbations during standing. The directional acuity threshold to lateral deviations in backward support-surface motion in healthy, young adults was quantified as  $9.5 \pm 2.4^\circ$  using the psychometric method ( $n = 25$  subjects). However, inherent limitations in the psychometric method, such as a large number of required trials and the predetermined stimulus set, may preclude wider use of this method in clinical populations. Our second goal was to validate an adaptive algorithm known as parameter estimation by sequential testing (PEST) as an alternative threshold estimation technique to minimize the required trial count without predetermined knowledge of the relevant stimulus space. The directional acuity threshold was estimated at  $11.7 \pm 3.8^\circ$  from the PEST method ( $n = 11$  of 25 subjects, psychometric threshold =  $10.1 \pm 3.1^\circ$ ) using only one-third the number of trials compared to the psychometric method. Furthermore, PEST estimates of the directional acuity threshold were highly correlated with the psychometric estimates across subjects ( $r = 0.93$ ) suggesting that both methods provide comparable estimates of the perceptual threshold. Computational modeling of both techniques revealed similar variance in the estimated thresholds across simulations of about  $1^\circ$ . Our results suggest that the PEST algorithm can be used to more quickly quantify whole-body directional acuity during standing in individuals with balance impairments.

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## 1. Introduction

Perceptual awareness of body motion may play an important role in balance control, particularly in sensorimotor-impaired individuals who may rely more heavily on attentional resources to maintain balance. Although balance may be primarily regulated through automatic, brainstem-mediated processes in healthy individuals [1], balance can be voluntarily controlled, such as when walking in challenging conditions [2]. Older adults and individuals with balance impairments have been shown to rely more heavily on attentional mechanisms during standing,

presumably to compensate for deficits in automatic postural control [3]. Therefore conscious perception of whole-body directional motion during standing may be important for individuals with balance impairments. Directional perception may be important for generating the appropriate directionally-dependent motor responses after a loss of balance [1,4].

However, perception of directional acuity of body motion during standing has not been previously been measured. Motion detection thresholds during standing have been quantified across different perturbation parameters (direction, displacement, jerk) with respect to the presence or the absence of a stimulus [5,6]. Subjective perception of natural sway during standing has also been linked to subjective perception of stability [7]. However, these studies do not provide precise information about the perception of the direction of body movement. In seated subjects, directional motion perception has been measured by determining their ability to discriminate differences in heading direction using

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suprathreshold perturbations [8]. Similar methods have been used to identify discrimination thresholds for single-joint motions and other perceptual tasks as well [9].

Identifying perceptual thresholds can be time consuming, and therefore not feasible in balance-impaired individuals. Traditionally, the two-alternative forced choice (2AFC) paradigm tests a large number of pairs of stimuli to construct a psychometric curve [10]. Generating a full psychometric curve requires a large number of stimuli as well as prior knowledge about the approximate value of the perceptual threshold. As the perceptual threshold may differ widely across individuals with balance impairments, generating a full psychometric curve may not be practical or feasible given physical limitation of the participants. Adaptive methods systematically search the stimulus space based on the participant's perceptual responses until the threshold is identified. As such, adaptive methods do not require a priori knowledge about the values of the perceptual threshold and are capable of estimating the threshold with fewer trials than the psychometric method.

Here, our goals were 1) to quantify directional acuity during support-surface perturbation to standing in a healthy young population, and 2) to compare the reliability of standard psychometric methods versus an adaptive algorithm. We determined thresholds of directional acuity in backward support-surface perturbations (Torres-Oviedo and Ting 2007) during standing in healthy, young adults. We compared thresholds estimated using the psychometric method to the parameter estimation by sequential testing (PEST) method, used previously for identifying detection thresholds during standing [5], and determined whether fewer trials were necessary using PEST. Finally, we validated the reliability of the two methods over repeated tests through computer simulations.

## 2. Methods

### 2.1. Participants

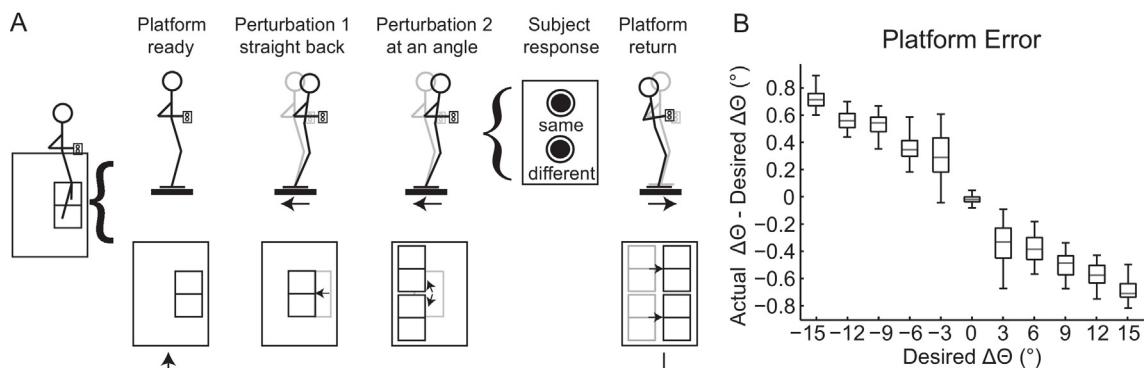
All experimental protocols were approved by the Institutional Review Boards of Georgia Institute of Technology and Emory University. Written informed consent was obtained from all participants before they were enrolled in the experiment. A total of twenty-five healthy young adults (mean age  $21.8 \pm 3.0$  years), consisting of 12 females and 13 males, were recruited to participate in the experiment. All participants were required to be 18 years of age and must not have had any history of musculoskeletal disorders, neurologic disorders, or dizziness as assessed by a self-report. In

addition, all participants were required to be native English speakers in order to limit the confounding effect of language learning on spatial perception [11].

### 2.2. Experimental protocol

During the experiment, participants stood on a translating platform used to present stimuli (Fig. 1A). Participants were blindfolded and wore headphones that played white noise to eliminate auditory and visual information, thus limiting the subject to proprioceptive, vestibular and somatosensory cues. Stance width was standardized for participants by having the middle of their heels positioned at a distance that matched their inter-anterior superior iliac spine (ASIS) distance. The participant's stance width was marked in order to maintain consistency throughout the experiment. The first platform translations, or perturbation, was always straight back ( $\Theta = 270^\circ$ ) while the second perturbation ranged from  $245^\circ$  to  $295^\circ$  ( $\Delta\Theta = \pm 25^\circ$  from the first perturbation) where  $0^\circ$  represents rightward perturbation and  $180^\circ$  represents leftward perturbation. The actual platform movement was analyzed relative to the desired platform movement (Fig. 1B) to quantify the accuracy of the platform motion. The error between the actual  $\Delta\Theta$  and desired  $\Delta\Theta$  increased with the amplitude of the desired  $\Delta$  ( $\Delta\Theta = 15^\circ$ , mean error =  $0.71^\circ$ ), but the precision of the platform (interquartile range =  $[0.04, 0.25]^\circ$ ) was sufficient to present functionally distinct stimulus perturbations at a resolution of  $0.5^\circ$ .

Each trial in the experiment consisted of two perturbations in which the participant was asked to determine whether or not the two perturbations were in the same or different direction. Each perturbation had a displacement of 7.5 cm, a velocity of 15 cm/s, and a peak acceleration of  $0.1 \text{ m/s}^2$ . The direction, or lateral deviation, of the second perturbation ( $\Delta\Theta$ ) for each trial was set by the psychophysical method used to determine the sensory threshold: the psychometric method or the parameter estimation by sequential testing (PEST) method [10]. The subject was not informed that the first perturbation was always in the backward direction ( $\Theta = 270^\circ$ ), nor when the first perturbation would occur (the time between the two perturbations was fixed at 0.5 s). After the second perturbation, the subject responded 'same' or 'different', by pressing a button on a response box that was held throughout each trial, to indicate whether the two perturbations were in the same or different direction. A trial was excluded if the subject took a step or did not respond in the given amount of time (3 s). Excluded trials were repeated at a later time. Due to



**Fig. 1. Experimental paradigm.** (A) Participants stood on a translating platform without auditory or visual feedback. Each trial consisted of two perturbations that varied only in the direction of the perturbation (Displacement = 7.5 cm, Velocity = 15 cm/s, Peak Acceleration =  $0.1 \text{ m/s}^2$ ). The first perturbation was straight back ( $270^\circ$ ), and the direction of the second perturbation varied relative to the first perturbation ( $255\text{--}295^\circ$ ,  $\Delta\Theta = \pm 25^\circ$ ). After the second perturbation, the participants reported whether the perturbations were in the 'same' or 'different' direction in each trial. The trial was completed when the platform then returned to a starting position. The session ended when a threshold was reached through either the PEST or psychometric method. (B) The platform movement error scaled with the amplitude of the desired stimulus ( $\Delta\theta$ ), but the variability of the platform movement was less than  $1^\circ$ .

limitation in the total travel of the perturbation platform, after each subject response, the platform was translated in the forward direction to prepare for the next trial (time between trials was randomized). This return movement was always in the 90° direction (straight forward) without any lateral deviation to prevent the subject from receiving feedback about the lateral movement of the two previous perturbations. Thus the initial absolute position of the platform varied in the lateral direction by a small amount. However subjects were blindfolded and thus did not receive any external cues about absolute position in the room.

Each experiment consisted of either the psychometric method alone ( $n = 14$  subjects) or 2+ PEST runs and one full psychometric run in the following order: first PEST run, half of the psychometric stimulus set, second PEST run, and last half of the psychometric stimulus set ( $n = 11$  subjects). If time permitted, a third PEST run was completed ( $n = 8$  of 11 subjects). Subjects were required to rest after each section of the experiment or by request. The psychophysical methods were interleaved to prevent long-term adaptation effects, such as fatigue, which could bias the data. The estimated threshold from the first PEST run provided a relevant stimulus range for each subject such that the  $\Delta\theta$  stimulus set chosen for the psychometric curve would include the threshold.

### 2.3. Psychometric method

For the psychometric method [12], a pre-determined set of stimulus conditions,  $\Delta\theta$ , were randomly presented to the subject to determine a directional acuity threshold. The stimuli consisted of 0° and five different  $\Delta\theta$  values ranging  $\pm 25^\circ$  from the cardinal direction (ex.  $\pm 15^\circ$ ,  $\pm 12^\circ$ ,  $\pm 9^\circ$ ,  $\pm 6^\circ$ ,  $\pm 3^\circ$  and 0°) with each presented 9 times [9]. The negative values represent angles that were to the left of the cardinal direction, while the positive values represent angles to the right. The stimulus set used in the psychometric method was chosen to include the estimated threshold from the first PEST run. The session ended when ninety-nine successful trials were recorded. Psychometric curves were fit to the measured response probabilities [13]. The threshold was estimated at the 75th percentile because chance response probability is 50% in a 2AFC task [14] (Fig. 2).

### 2.4. Parameter estimation by sequential testing method

As opposed to the psychometric method, which uses pre-selected  $\Delta\theta$  values, the PEST method employs a standard 2D1U (2-down-1-up) adaptive algorithm that chooses  $\Delta\theta$  values for each trial based on the subject's responses to the previous trials. The  $\Delta\theta$  changes on each trial in an increment that is equal to the current

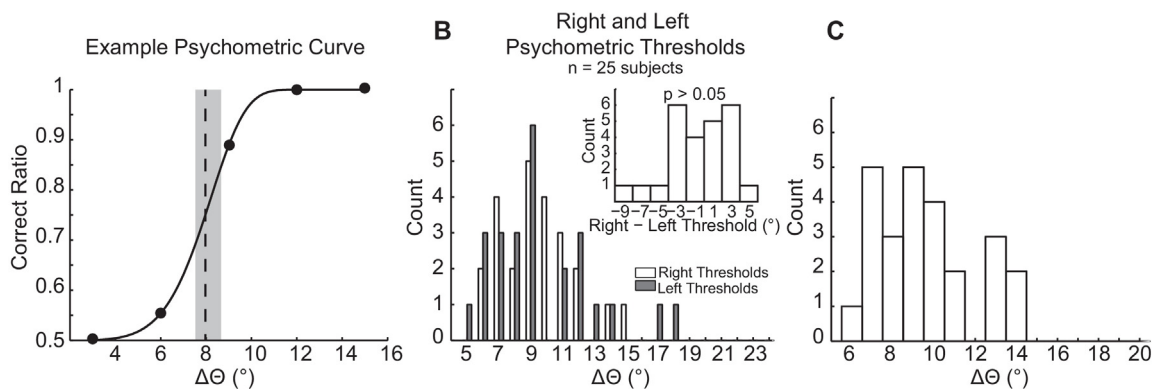
step size. The current step size changes based on the subject's previous responses [15] and the session ends when the iterative step size falls to 0.5° or lower. An initial  $\Delta\theta$  of +3° or -3°, an initial step size of 4°, and a stopping step size criterion of 0.5° were used for each PEST run [5]. The 2D1U PEST method was chosen to target a 75% threshold [5]. Multiple PEST thresholds were estimated for each subject to validate the accuracy of PEST for measuring directional acuity thresholds as well as the stability of the threshold estimate over an experimental period ( $n = 3$  subjects with 2 PEST runs;  $n = 8$  subjects with 3 PEST runs). The recovered thresholds quantified in Fig. 3 were estimated from the first PEST run.

### 2.5. Data analysis

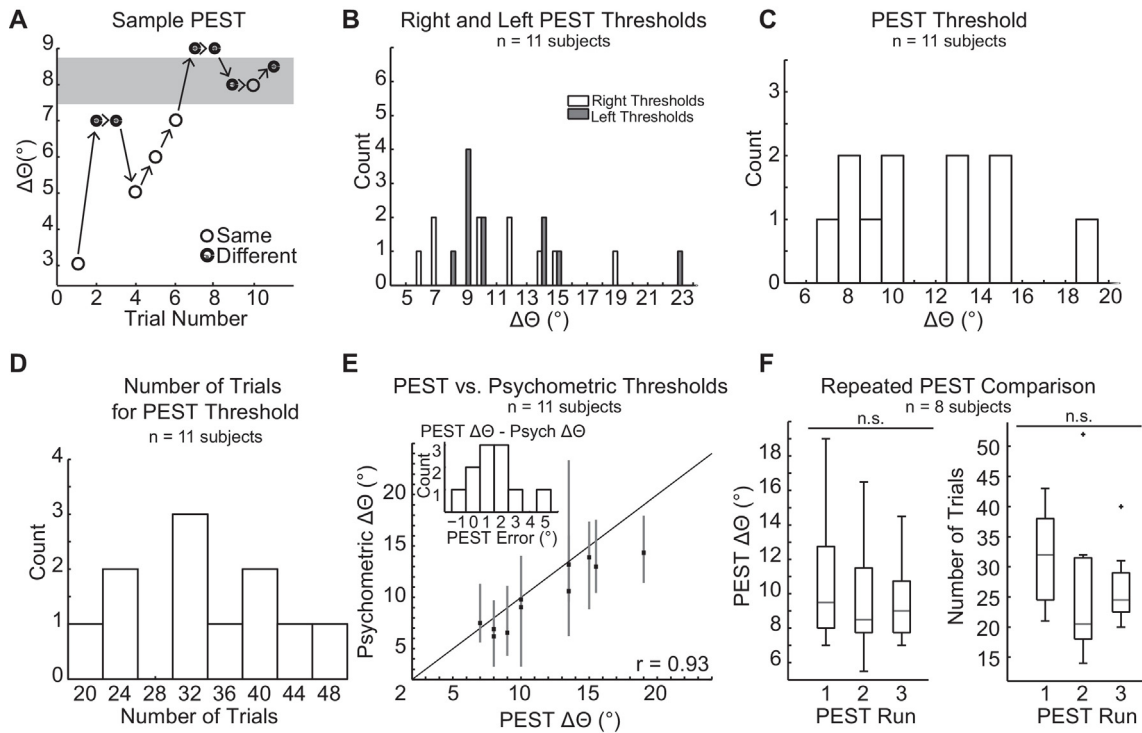
For the psychometric method, the response data was analyzed using the Wichmann toolbox MATLAB code to determine the 75% probability threshold and the 95% confidence interval [13]. The threshold for the PEST method was estimated as the  $\Delta\theta$  that was tested when the step size reached 0.5° [5]. A paired  $t$ -test was used to compare the left and right thresholds estimated from both the psychometric and PEST methods. The correlation between the psychometric thresholds and PEST thresholds was used to determine the similarity in the threshold estimation techniques. The multiple PEST runs were compared using a one-way repeated measures ANOVA to determine whether the estimated threshold or the number of trials varied across PEST runs.

### 2.6. Computational modeling

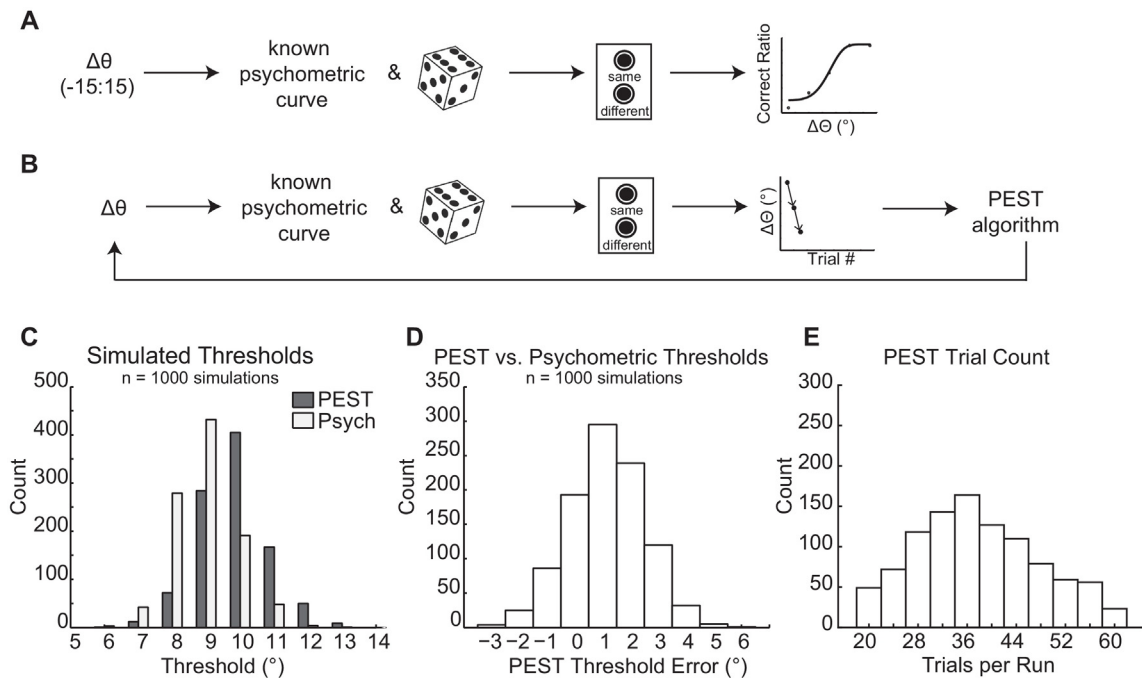
A computational model was developed to simulate the responses of a subject to the psychometric and PEST protocols based on their measured psychometric curve. The simulation assumes that an experimentally measured psychometric curve represents the true directional acuity for the simulated subject; it does not account for nonstationary response properties such as fatigue. The simulated subject's response to each trial was probabilistic such that the probability of response was determined by the measured psychometric curve. The experimental paradigm was mimicked in simulation to estimate of the variability of both psychometric (Fig. 4A) and PEST (Fig. 4B) methods. At a given stimulus intensity, a random number was generated (uniform distribution (0,1)) and the binary response of 'same' or 'different' was based on the probability of correct response from the psychometric curve; random numbers lower than the probability of correct response were labeled as 'different'. The directional acuity threshold of the simulated subject was estimated 1000 times



**Fig. 2. Psychometric thresholds.** (A) An example psychometric curve from one subject with a directional acuity threshold of 8.0°. (B) Using the psychometric method, a threshold was reached for perturbations to the left and right of center ( $n = 99$  trials). Left and right thresholds were not significantly different ( $n = 25$  subjects,  $p = 0.52$ , paired  $t$ -test). (C) The left and right thresholds were averaged together to quantify an overall psychometric threshold of  $9.5 \pm 2.4^\circ$  ( $n = 25$  subjects).



**Fig. 3. PEST thresholds.** (A) An example PEST run from one subject with an estimated threshold of  $8.5^\circ$ . (B) The right and left PEST thresholds measured in the first PEST run were not significantly different ( $n = 11$  subjects,  $p = 0.37$ , paired  $t$ -test). (C) The right and left PEST thresholds were averaged together to measure an overall PEST threshold of  $11.7 \pm 3.8^\circ$  ( $n = 11$  subjects). (D) The average number of trials needed to reach a left and right PEST threshold for the first PEST iteration was  $33.8 \pm 8.4$  trials ( $n = 11$  subjects). (E) The first PEST threshold is highly correlated with the psychometric threshold for each subject ( $r = 0.93$ ). Error bars represent three standard deviations of the psychometric threshold estimate. Inset depicts the PEST threshold estimate relative to the psychometric threshold as quantified by the number of degrees the PEST estimate is away from the psychometric threshold. (F) Multiple PEST runs were measured for a single subject ( $n = 8$  subjects). The PEST threshold estimate and the number of trials required to reach a threshold were not significantly different across PEST iterations (n.s. =  $p > 0.05$ , one-way repeated measures ANOVA).



**Fig. 4. Computational model of PEST and psychometric method.** (A) The psychometric model simulated a subject response using a measured psychometric curve from one subject (threshold =  $8.9^\circ$ ). All parameters of the psychometric simulation matched the experimental parameters ( $\Delta\theta = \pm 15^\circ$ ,  $n = 9$  samples per stimulus condition). The simulation was run 1000 times ( $n = 1000$  estimated simulated psychometric thresholds). (B) The PEST model was built from the same assumed psychometric curve used in (A). Experimental PEST parameters ( $\Delta\theta_{\text{initial}} = 1^\circ$ , step size =  $4^\circ$ ) were simulated 1000 times ( $n = 1000$  estimated simulated PEST thresholds). (C) Across 1000 samples from a single simulated subject, the simulated PEST threshold was  $10.1 \pm 1.0^\circ$  and the simulated psychometric threshold was  $8.9 \pm 0.9^\circ$ . (D) The simulated PEST thresholds were compared to the simulated psychometric thresholds to assess the variability of the measures on a trial-to-trial basis. The simulated PEST thresholds fell within a range of  $-3^\circ$  to  $6^\circ$  of the psychometric threshold on any given simulation from the same simulated subject. (E) The average number of trials required to reach a PEST threshold was  $38.3 \pm 10.0$  trials.



to generate 1000 estimated thresholds of a single simulated subject for both the psychometric and the PEST methods.

### 3. Results

#### 3.1. Psychometric thresholds

The direction discrimination threshold was  $9.5 \pm 2.4^\circ$  in 25 subjects using the psychometric method. An example of a one-sided directional acuity threshold, measured using the psychometric method for a sample subject is shown in Fig. 2A ( $\Delta\theta_{\text{thres}} = 8.0^\circ$ , left threshold). Across subjects ( $n = 25$ ), there was no statistically significant difference between the left and right directional acuity thresholds ( $p = 0.52$ ) (Fig. 2B). Therefore, the overall directional acuity threshold was defined to be the average of the left and right thresholds. The threshold for this population was  $9.5 \pm 2.4^\circ$ , while the range was from  $6.2^\circ$  to  $14.4^\circ$  ( $n = 25$  subjects, Fig. 2C).

#### 3.2. PEST thresholds compared to psychometric thresholds

The direction discrimination threshold was  $11.7 \pm 3.8^\circ$  in 11 subjects using the PEST method using about a third of the trials compared to the psychometric method. An example one-sided PEST run from the same subject as in Fig. 2A terminated after only 11 trials and estimated a threshold of  $8.5^\circ$  which is within the 95% confidence interval of the psychometric threshold estimate (Fig. 3A; shaded bar represents confidence interval from the psychometric curve). Across subjects, there was no significant difference between the left and right PEST thresholds ( $p = 0.37$ ,  $n = 11$  subjects) (Fig. 3B). Therefore, as with the psychometric method, the left and right PEST thresholds were averaged together to measure an overall PEST threshold of  $11.7 \pm 3.8^\circ$  (Fig. 3C). An average of  $33.8 \pm 8.4$  trials were required to measure the overall PEST thresholds for PEST run 1 (Fig. 3D).

The PEST estimated thresholds were highly correlated with the psychometric thresholds across subjects ( $r = 0.93$ , Fig. 3E), and 90.9% of the PEST run 1 thresholds fell within  $\pm 3^\circ$  of their corresponding psychometric threshold (Fig. 3E inset). However, the PEST estimated thresholds were significantly different from the psychometric thresholds because PEST systematically estimated a larger threshold than the psychometric method ( $p = 0.005$ , paired  $t$ -test). Comparison of multiple PEST runs within the same subject found that the PEST threshold estimate and the number of perturbations required to reach threshold was not significantly different between each of the three PEST runs ( $n = 8$  subjects) (Fig. 3F).

#### 3.3. Computational model of PEST and psychometric methods

Using a simulated subject with a known threshold of  $8.9^\circ$ , model thresholds were identified as  $8.9 \pm 0.9^\circ$  using the psychometric method and  $10.1 \pm 1.0^\circ$  using the PEST method (Fig. 4C). Importantly, the variability in the psychometric and PEST threshold estimates are comparable (standard deviation = 0.9,  $1.0^\circ$  respectively). Although the comparison between the psychometric threshold and the PEST threshold on any given trial is variable, 92% of the estimated PEST thresholds fell within  $\pm 3^\circ$  of their corresponding psychometric threshold (Fig. 4D). The simulated PEST method converged to a threshold within  $38.3 \pm 10.0$  trials (Fig. 4E). Both the variability of PEST relative to psychometric and the required trial count for PEST are comparable to the experimental conditions (Fig. 3D and E).

### 4. Discussion

Here we present the first known quantification of directional acuity thresholds during perturbations to standing in a healthy young adult population. Standing balance requires multisensory

integration of vestibular, proprioceptive, cutaneous, and visual cues [1]; visual and auditory cues were eliminated in our protocol. The directional acuity threshold of  $9.5 \pm 2.4^\circ$  for full body perturbations was higher than those of individual joints, such as hip flexions ( $2.3^\circ$  threshold) and knee movements ( $3.8^\circ$  threshold), and higher than discrimination thresholds for seated subjects of heading direction isolating vestibular afferents, although contributions of cutaneous afferents cannot be avoided ( $6.0^\circ$  threshold) [16–18]. Typically, when more than one sensory modality is available, such as visual and proprioceptive input, subjects tend to achieve thresholds that are equivalent to the modality with the greatest acuity [6]. Moreover, according to optimal estimation theory, multiple inputs can be combined to provide estimates that are better than a single sensory modality [19]. However, larger thresholds to whole body perturbations could be due to the fact that multiple joint motions must be estimated. Additionally, perceptual thresholds due to cutaneous stimulation of the foot sole are elevated in standing compared to sitting [20], and spinal responses to muscle spindle input are also reduced in standing compared to sitting [21]. Additionally, tactile thresholds are increased in the presence of muscle activity [22,23]; proprioceptive afferents, i.e. muscle spindles and Golgi tendon organs, may be similarly affected by muscle activity when the sensory stimulus is delivered [24,25]. Postural sway could also induce sensory input, affecting estimated perceptual thresholds [6,7]. Moreover, we do not know how direction acuity might vary as a function of perturbation characteristics; larger perturbations causing near-falls could be harder to discriminate, whereas smaller perturbations could be less salient. Further work on the biomechanical and sensory information underlying directional perception is warranted.

Both experimental and computational comparisons of PEST to the psychometric method suggest that the PEST algorithm may be an efficient method to estimate directional acuity in a short amount of time. Experimentally-derived perceptual thresholds were highly correlated ( $r^2 = 0.87$ ) although PEST estimates were consistently larger than those found through the psychometric method. Computational results showed that PEST tended to overestimate ground-truth thresholds by about  $1^\circ$  using our protocol. This may be because the psychometric method estimates the threshold based on a curve fit to responses at all stimulus magnitudes, whereas the PEST algorithm approximates the threshold through sequential testing of stimuli near the threshold. The reliability of the PEST estimates over repeated simulations was comparable to those found using the psychometric method, with standard deviations of about  $1^\circ$ . However, PEST was able to identify thresholds in about one-third to one-half the number of trials that we used for the psychometric method. While other adaptive methods have been used to more accurately quantify sensory thresholds through dense sampling of the stimulus space near the threshold, they do not significantly lower the number of trials [26,27]. A limitation of the PEST method is that it cannot provide information about the shape of the psychometric curve.

Directional acuity testing during standing may provide important information about the relative contributions of sensory versus motor deficits to fall risk in balance-impaired populations. Perceptual deficits in awareness of body motion rather than motor coordination could cause incorrect motor responses in a wide range of clinical populations with sensorimotor impairments such as people with Parkinson's disease (PD), stroke, diabetes, multiple sclerosis, and in typically aging adults who may be at risk for falls. As the PEST method does not require prior knowledge about the amplitude of the sensory threshold and can be performed relatively quickly, it may be useful for exploring deficits in body motion perception. Although, we found no difference between left and right directional acuity thresholds, these would be expected to differ in lateralized diseases such as PD and stroke. As both sensory and motor deficits are increasingly being recognized in a variety of

sensorimotor disorders, testing whole-body direction acuity may be important to understanding and treating balance disorders.

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## References

- [1] MacPherson JM, Horak FB. Posture. In: Kandel ER, Schwartz JH, Jessell TM, Siegelbaum SA, Hudspeth AJ, editors. *Princ Neural Sci*. 5th ed., McGraw-Hill; 2012. p. 935–59.
- [2] Sawers A, Ting LH. Beam walking can detect differences in walking balance proficiency across a range of sensorimotor abilities. *Gait Posture* 2015;41:619–23. <http://dx.doi.org/10.1016/j.gaitpost.2015.01.007>.
- [3] Woollacott M, Shumway-Cook A. Attention and the control of posture and gait: a review of an emerging area of research. *Gait Posture* 2002;16:1–14. [http://dx.doi.org/10.1016/S0966-6362\(01\)00156-4](http://dx.doi.org/10.1016/S0966-6362(01)00156-4).
- [4] Oude Nijhuis LB, Allum JHJ, Borm GF, Honegger F, Overeem S, Bloem BR. Directional sensitivity of “first trial” reactions in human balance control. *J. Neurophysiol.* 2009;101:2802–14. <http://dx.doi.org/10.1152/jn.90945.2008>.
- [5] Richerson SJ, Faulkner LW, Robinson CJ, Redfern MS, Purucker MC. Acceleration threshold detection during short anterior and posterior perturbations on a translating platform. *Gait Posture* 2003;18:11–9. [http://dx.doi.org/10.1016/S0966-6362\(02\)00189-3](http://dx.doi.org/10.1016/S0966-6362(02)00189-3).
- [6] Fitzpatrick R, McCloskey DI. Proprioceptive, visual and vestibular thresholds for the perception of sway during standing in humans. *J. Physiol.* 1994;478:173–86.
- [7] Schieppati M, Tacchini E, Nardone a, Tarantola J, Corna S. Subjective perception of body sway. *J. Neurol Neurosurg. Psychiatry* 1999;66:313–22. <http://dx.doi.org/10.1136/jnnp.66.3.313>.
- [8] Gianna C, Heimbrand S, Gresty M. Thresholds for detection of motion direction during passive lateral whole-body acceleration in normal subjects and patients with bilateral loss of labyrinthine function. *Brain Res. Bull.* 1996;40:443–9. [http://dx.doi.org/10.1016/0361-9230\(96\)00140-2](http://dx.doi.org/10.1016/0361-9230(96)00140-2).
- [9] Blake R, Sekuler R. Perception. In: Barrosse E, editor. *Perception*. 5th ed, New York: McGraw-Hill; 2006. p. 553–68.
- [10] Ehrenstein WH, Ehrenstein A. Psychophysical methods. *Mod. Tech. Neurosci. Res.* 1999;1211–41. [http://dx.doi.org/10.1007/978-3-642-58552-4\\_43](http://dx.doi.org/10.1007/978-3-642-58552-4_43).
- [11] Hayward WG, Tarr MJ. Spatial language and spatial representation. *Cognition* 1995;55:39–84. [http://dx.doi.org/10.1016/0010-0277\(94\)00643-Y](http://dx.doi.org/10.1016/0010-0277(94)00643-Y).
- [12] Wichmann FA, Hill NJ. The psychometric function: I. Fitting, sampling, and goodness of fit. *Percept Psychophys.* 2001;63:1293–313. <http://dx.doi.org/10.3758/BF03194544>.
- [13] Fründ I, Haenel NV, Wichmann FA. Inference for psychometric functions in the presence of nonstationary behavior. *J. Vis.* 2011;11:1–19. <http://dx.doi.org/10.1167/11.6.16>.
- [14] Harvey LO. Efficient estimation of sensory thresholds. *Behav. Res. Methods Instruments Comput.* 1986;18:623–32. <http://dx.doi.org/10.3758/BF03201438>.
- [15] Taylor MM, Creelman CD. PEST: efficient estimates on probability functions. *J. Acoust. Soc. Am.* 1967;41:782–7. <http://dx.doi.org/10.1121/1.1910407>.
- [16] Refshauge KM, Fitzpatrick RC. Perception of movement at the human ankle: effects of leg position. *J. Physiol.* 1995;488:243–8.
- [17] Refshauge KM, Chan R, Taylor JL, McCloskey DI. Detection of movements imposed on human hip, knee, ankle and toe joints. *J. Physiol.* 1995;488:231–41. <http://dx.doi.org/10.1113/jphysiol.1995.sp020961>.
- [18] MacNeilage PR, Banks MS, DeAngelis GC, Angelaki DE. Vestibular heading discrimination and sensitivity to linear acceleration in head and world coordinates. *J. Neurosci.* 2010;30:9084–94. <http://dx.doi.org/10.1523/JNEUROSCI.1304-10.2010>.
- [19] van der Kooij H, Jacobs R, Koopman B, Grootenboer H. A multisensory integration model of human stance control. *Biol. Cybern.* 1999;80:299–308. <http://dx.doi.org/10.1007/s004220050527>.
- [20] Mildren RL, Strzalkowski NDJ, Bent LR. Foot sole skin vibration perceptual thresholds are elevated in a standing posture compared to sitting. *Gait Posture* 2015. <http://dx.doi.org/10.1016/j.gaitpost.2015.10.027>.
- [21] Hayashi R, Tako K, Tokuda T, Yanagisawa N. Comparison of amplitude of human soleus H-reflex during sitting and standing. *Neurosci. Res.* 1992;13:227–33. [http://dx.doi.org/10.1016/0168-0102\(92\)90062-H](http://dx.doi.org/10.1016/0168-0102(92)90062-H).
- [22] Jiang W, Lamarre Y, Chapman CE. Modulation of cutaneous cortical evoked potentials during isometric and isotonic contractions in the monkey. *Brain Res.* 1990;536:69–78.
- [23] Chapman CE, Beauchamp E. Differential controls over tactile detection in humans by motor commands and peripheral reafference. *J. Neurophysiol.* 2006;96:1664–75. <http://dx.doi.org/10.1152/jn.00214.2006>.
- [24] Dimitriou M. Human muscle spindle sensitivity reflects the balance of activity between antagonistic muscles. *J. Neurosci.* 2014;34:13644–55. <http://dx.doi.org/10.1523/JNEUROSCI.2611-14.2014>.
- [25] Horcholle-Bossavit G, Jami L, Petit J, Vejsada R, Zytynicki D. Ensemble discharge from Golgi tendon organs of cat peroneus tertius muscle. *J. Neurophysiol.* 1990;64:813–21.
- [26] Watson AB, Pelli DG. QUEST: a Bayesian adaptive psychometric method. *Percept. Psychophys.* 1983;33:113–20. <http://dx.doi.org/10.3758/BF03202828>.
- [27] Elangovan N, Herrmann A, Konczak J. Assessing proprioceptive function: evaluating joint position matching methods against psychophysical thresholds. *Phys. Ther.* 2014;94:553–61.