Activation of ankle muscles following rapid displacement of a light touch contact during treadmill walking.

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Abstract

The first exposure of a rapid displacement of a light touch reference induces an inappropriate balance corrective response during standing in a proportion of participants that is extinguished with repeated exposures. We hypothesized that if the spatial touch reference was critical to performing of a task the evoked response would be more consistently expressed across participants and observed with repeated exposures to the disturbance. To test this, twenty participants received either forward (N=10) or backward right touch displacements at right heel strike during motorized treadmill walking without visual feedback. Electromyographic recordings from 4 arm, 4 leg and 1 neck muscle were sampled along with joint kinematic and step cycle data. Rapid displacement of the touch surface elicited responses in all 20 participants. However, the frequency of first trial responses was not different from what was observed during standing. In contrast, responses were observed in all participants with subsequent trials. None of the participants tripped or stumbled as a result of the touch perturbations, however the step cycle duration was consistently shorter following the first forward touch displacement. A post-experiment questionnaire revealed that many participants often perceived the touch plate displacement as a disturbance to the treadmill belt speed, suggesting the disturbance was occasionally misinterpreted. The activation of ankle muscles following the unexpected slip of a touch reference during walking suggests that tactile information from the finger is a relevant sensory cue for the regulation and control of stepping and stability.

Keywords: haptic, touch, walking, locomotion, human, gait

Introduction

A common strategy employed by humans when balance becomes challenging is to grab an external support with their hands. The mechanical benefit of holding an aid with the hands provides stability by increasing the area of the base of support. In addition to the mechanical benefit offered by holding an aid, the contact of the hand to an external support also presents the potential for increased sensory feedback as the hands are endowed with a rich sensory field. It is well documented that lightly touching (<1 N of vertical force) a stationary surface with a fingertip reduces postural sway in quiet standing with eyes closed (Jeka and Lackner 1994). Touch of < 1N is argued to be insufficient to provide mechanical stabilization (Holden et al. 1994; Kouzaki and Masani 2008), but could provide additional sensory inputs from the skin. In addition, it has been shown that imperceptible oscillation of the touch reference will entrain the sway of the body to the movement of the touch reference (Jeka et al. 1997). This suggests that shear forces at the fingertip might provide an important sensory cue about the motion of the body relative to an external reference that is integrated within the balance control system. Taken together, these findings indicate that light touch of the fingertip provides a supplementary sensory cue that is integrated within the balance control system, contributing to the regulation of the postural sway and maintaining a stable body position while standing.

Recently, we demonstrated that unexpected forward displacement of a light touch reference evoked postural responses in tibialis anterior (TA) in 12 of 20 participants (Misiaszek et al. 2016). However, the responses observed in TA following the touch displacement were only observed following the initial displacement. It was suggested that the absence of a response in TA in the subsequent trials or the lack of responses observed in some participants reflected a context-dependent weighting of the tactile feedback. That is, the incorporation of tactile feedback in balance control is not required for successful performance of the task of standing upright. Therefore, some participants may have placed a greater weighting on the tactile feedback than others that was then adjusted once the participants became aware the touch reference was unreliable. If so, then increasing the importance of the tactile feedback to the ability to maintain stability should result in more consistent expression of postural responses across participants and with repeated trials.

In this study, we increased the relevance of the light touch reference by asking participants to walk on a motorized treadmill with their eyes closed, while touching a reference.

Participants walking on a motorized treadmill with their eyes closed will drift towards the back of the treadmill without a spatial reference (Durgin and Pelah 1999; Paquet et al. 2000; Dickstein and Laufer 2004). However, this backward drift is eliminated when participants are provided with a light touch reference (Dickstein and Laufer 2004; Forero and Misiaszek 2013). In this context, the cutaneous feedback from the fingertip is of critical importance as contact with the spatial reference is the only indicator of the position of the participant on the treadmill. As the participant's position moves relative to the spatial reference, shear forces at the fingertip will be generated by the movement. Our expectation is that if the light touch contact surface is unexpectedly displaced, this signal will be interpreted as though the participant has moved relative to the spatial reference and the corresponding correction will be activated. Moreover, balance corrective responses that are induced by pulls to the waist during treadmill walking are facilitated when participants are provided a light touch reference (Forero and Misiaszek 2013), supporting the hypothesis that integration of light touch feedback contributes to balance control during walking. Therefore, we hypothesized that, 1) short latency (<200 ms) responses will be evoked in the ankle muscles with an unexpected displacement of a touch reference; and 2) these responses would be observed more frequently than what was observed previously during standing (Misiaszek et al. 2016).

Materials and Methods

Participants

Twenty participants (aged 18-35, 14 females) volunteered to participate in this study. Subjects reported no history of neurological, musculoskeletal, metabolic or cardiovascular disease, and had not experienced musculoskeletal injury, back pain, or concussion in the past 6 months. All participants provided written informed consent, and the project was approved by the University of Alberta Research Ethics Board in accordance with the Declaration of Helsinki.

Protocol

In this study, we wished to directly compare the frequency of response occurrence during treadmill walking with that observed during standing from our previous study (Misiaszek et al. 2016). Consequently, the protocol, stimulus delivery, data acquisition and data analysis procedures used previously were replicated here, but adapted for the task of walking on a treadmill. For example, we previously used a slow oscillation of the touch apparatus to entrain the sway of standing participants to ensure the rapid touch displacement was delivered at a consistent point in the sway cycle. During treadmill walking, the fore-aft motion of the body center of mass is naturally entrained to the step cycle and therefore, the delivery of the rapid touch displacement in the present study was delivered at a consistent point in the step cycle.

To emphasize the unexpected nature of the displacement of the touch reference, participants performed a series of decoy tasks in addition to the test task. For all tasks, participants walked on a motorized treadmill (Quinton Instruments Model 18-60, Seattle, Washington, USA), at a self-selected speed (range: 0.9 to 1.2 m/s). Because one of the decoy tasks involved walking on the treadmill with eyes closed and without touching a spatial reference, participants were first trained to walk on the treadmill with eyes closed. During this training period manual guidance of the torso and verbal cueing was provided to ensure that participants did not drift towards the back or sides of the treadmill belt. The walking speed selected for all tasks was determined as the speed the participant was comfortable with when walking with eyes closed and without assistance. Participants wore a safety belt that limited the distance they might fall vertically, but placed no restriction on their fore-aft or medial-lateral movements. A spotter was present throughout all trials. The decoy tasks consisted of three walking conditions: 1) with eyes open and arms swinging normally; 2) with eyes closed and arms swinging normally; and 3) with eyes open while lightly touching (<1 N) a touch plate located in front of their position on the treadmill, biased toward the right arm (Fig. 1A). Each decoy task was 1 min in duration and participants rested for 1 min between each.

During the test task, participants walked on the treadmill with eyes closed and while lightly touching the touch plate. After approximately 30 s of walking the touch plate was unexpectedly displaced targeting right heel strike (see *Set-up and apparatus*). The direction of the touch plate displacement (forward or backward) was randomized between participants such that 10 participants received forward displacements only and another 10 received backward displacements only. Each participant received 10 displacement trials of the touch plate, all of which were delivered targeting right heel strike. Between displacements, the touch plate was slowly repositioned (5 seconds) to the initial reference point, while the participant continued to maintain contact with the touch plate. The next displacement was delivered randomly between 5 and 10 steps after the touch plate had been repositioned to the original position. Typically, this resulted in the delivery of a displacement once every 35 to 45 s. The test task lasted up to 10 min.

Set-up and apparatus

The touch plate consisted of a 3.75 cm× 7.5 cm brushed aluminium plate, mounted on a steel rod that allowed for the height of the touch plate to be adjusted. The right index finger was held vertical on the center of the touch plate, and the forearm was held approximately horizontal by maintaining the right wrist in a neutral position (Fig. 1A). The elbow was flexed at 90° and a neutral position was maintained at the shoulder. In order to generate a linear displacement of the plate, the touch plate was mounted on a square rail acme screw drive positioning stage (Lintech Positioning Systems 130 Series, Monrovia, California, USA), driven by a computer-controlled two-phase stepper motor (Applied Motion Products 5023-124 2-phase hybrid step motor, Watsonville, California, USA). The onset of the displacements was manually triggered by a researcher to occur at approximately right heel strike. The touch plate was displaced by 12.5 mm, with a peak velocity of 124 mm/sec. The entire touch plate apparatus was mounted on top of a 6 component force plate (AMTI MC3A-100, Advanced Mechanical Technology, Inc., Watertown, Massachusetts, USA) to allow for the vertical component of the touch force to be measured. The touch force was monitored online and auditory feedback was provided if the force exceeded 1N. Participants were instructed to place the tip of the distal phalanx of their right index finger vertically on a raised dimple in the centre of the plate. The use of a raised dimple on the touch plate was necessary as pilot testing revealed that participants were unable to maintain their position on the treadmill with a smooth contact surface and would seek to contact the edges of the touch plate as a reference. As a consequence, they were instructed to curl the remaining fingers inside the palm, to avoid any supplemental contact with the touch plate. All participants were instructed to use their right hand to contact the touch plate, regardless of their hand dominance as the role of cutaneous feedback does not differ between hands in this context. In all tasks the left arm was free to swing naturally. Visual input was removed (eyes closed conditions) by asking the participants to wear a pair of darkened goggles. In addition, to mask any auditory cues that might be present during the operation of the motor, the participants were equipped with a pair of headphones and received white noise throughout the experiment.

Immediately after the test task, participants completed a questionnaire to evaluate what they had perceived during the test task. The questionnaire asked whether they had experienced any disturbance during the test task a) at their finger, b) at their waist, or c) of the treadmill belt. Subsequent questions asked details of what they reported experiencing including: the number of such perturbations; if the characteristics (amplitude, velocity) changed with repeated exposures; where within the duration of the test task the disturbances occurred; and other features of the experience. In addition, participants were asked to describe in their own words what they thought had happened. Following completion of the questionnaire the nature of the study's deception was fully disclosed.

Recording and Data Acquisition

Electromyographic (EMG) activity was recorded from the sternocleidomastoid (SCM), anterior deltoid (AD), posterior deltoid (PD), biceps brachii (BB) and triceps brachii (TB) muscles of the right arm; and tibialis anterior (TA), soleus (SOL), vastus lateralis (VL) and biceps femoris (BF) of the right leg. EMG activity was recorded using pairs of Ag/AgCl electrodes (NeuroPlus A10040, Vermed, Bellows Falls, Vermont, USA) placed on the skin over the bellies of the intended muscles, parallel to the predicted orientation of the muscle fibers, with an inter-electrode distance of about 2 cm. Ground electrodes were placed over the olecranon process of the right arm and on the anterior tibia of the right leg. Before the electrodes were applied, the skin over the muscle belly was shaved with a razor and cleaned with alcohol. The electrode site was then tested (Grass F-EZM5 impedance meter, Astro-Med, Inc., West Warwick, Rhode Island, USA) to ensure an impedance of less than 20 kΩ. The EMG signals were variably amplified and band-pass filtered (30 Hz-1 kHz with a 60 Hz notch filter, Grass P511 amplifiers, Astro-Med, Inc., West Warwick, Rhode Island, USA) prior to digitization. Electrogoniometers (Biometrics Ltd., Newport, UK) were placed across the right ankle, knee and elbow joints. Force-sensitive resistors (Interlink Electronics, Camarillo, California, USA) were placed on the insoles of both shoes under the heel and the head of the first metatarsal to record the foot contact data bilaterally. All analog signals were digitized at 4000 Hz (PCI-MIO-16E-4, National Instruments, Austin, Texas, USA) and stored to hard drive using a custom-written data acquisition routine (LabVIEW v. 8.2, National Instruments, Austin, Texas, USA).

Data Analysis

Data analysis was performed post-hoc using custom-written LabVIEW routines. The EMG signals were digitally full-wave rectified and low-pass filtered (50 Hz, 4th order zero-lag Butterworth filter). The mechanical signals were low-pass filtered (20 Hz, 2nd order zero-lag Butterworth filter). For the purpose of analysis, perturbed steps and control steps were extracted from the continuous data feed. For each step an 1800 ms trace was extracted and aligned at the right heel strike, including a period of 200 ms prior to the right heel strike. Perturbed steps are those in which the touch displacement occurred within ±100 ms of the right heel strike (Fig. 1B). (Note that all displacements were successfully delivered within this window). For each perturbed step the five steps preceding the perturbation were extracted as the control steps. From these five control steps average control traces were calculated along with the 95% confidence band. The average control traces were then subtracted from the perturbed traces to create subtracted traces for each individual touch plate displacement (Fig. 1C). A response in a particular muscle, or a disturbance in a goniometer trace, was identified when the subtracted trace exceeded the 95% confidence band for the average control trace for more than 25 ms continuously. The procedure for identifying the occurrence of a response varied from the approach used in Misiaszek et al. (2016), wherein a response was identified when the EMG of a muscle exceeded a two standard deviations band calculated from the mean EMG activity for the 100 ms prior to the displacement onset. This difference in analysis approaches was necessitated by the rhythmic oscillation and step to step variability in EMG activity that occurs during treadmill walking. The onset latency of a response was identified as the time when the subtracted trace began to deviate from the zero level. We selected the onset latency from within the confidence interval, rather than when the response escaped the band, because an active muscle will have a larger 95% confidence interval band and a delay will occur as the signal evolves to reach the confidence limits (Misiaszek 2003). For consistency with the approach used in Misiaszek et al. (2016), only responses with an onset latency <200 ms were included for further consideration. The response amplitude was measured as the mean amplitude of the subtracted trace over the 100 ms following response onset. EMG response amplitudes were expressed as a percentage of the participant's isometric maximum voluntary contraction (MVC).

Background EMG was calculated for the 50 ms before the onset of the touch plate displacement and expressed as a percentage of MVC. Step cycle, stance and swing durations were estimated bilaterally from the foot contact data from the perturbed steps, as well as the undisturbed (control) step immediately preceding. The vertical touch force was monitored throughout the experiment for each participant and maintained below 1 N. Mean background touch force was measured for the 50 ms prior to the onset of each touch displacement.

Statistics

The frequency of responses to touch plate displacements during walking were compared to the data from Misiaszek et al. (2016) for standing. Fisher's Exact Tests were used to compare the response frequencies for each muscle following the first trial between standing and walking. Frequency of responses in trials 2 through 10 were also compared between standing and walking. To determine if the evoked responses showed adaptation with repeated exposure to the touch plate displacement paired *t*-tests were used to compare the onset latency and amplitude of the first (α) and last evoked response (ω). As not all touch displacements resulted in identifiable responses, α and ω responses for a participant were not necessarily the first and last touch displacements. Paired *t*-tests were also used to compare the background EMG and touch force for the first response to that of the last response. Stance, swing and step cycle duration parameters were compared using separate one-way repeated measures analysis of variance (ANOVA) comparing control, trial 1 and trial 10. Bonferroni post-hoc comparisons were used to characterize differences identified by the ANOVA. Significant differences were identified when $p < 0.05$.

Results

Unexpected displacement of a touch plate evoked short-latency responses (<200 ms) in all 20 participants. All participants that received forward touch displacements reacted with activation of TA, expressed in 62/100 total trials. In contrast, backward displacements of the touch plate evoked responses in SOL in all participants, with responses expressed in 64/100 trials. It was rare to observe responses in SOL following forward displacements, or responses in TA following backward displacements. Responses in other leg muscles (VL and BF) were rare with fewer than 30/100 responses observed for forward or backward displacements. Responses in the arm muscles were also observed, but were generally rare, with the exception of responses in PD following backward displacements where all participants produced responses in at least 2 trials and responses were expressed in 56/100 total trials. Responses in SCM occurred in only 8/100 trials, and were never observed with the first exposure to a touch disturbance in any participant. The occurrence of responses is depicted in Figure 2 for forward displacements and in Figure 3 for backward displacements.

Response frequencies across trials

As shown in Figure 2, the first forward touch displacement evoked responses in TA in 7 out of 10 participants during treadmill walking. This is not significantly different (Fisher's Exact Test = 0.7) from the 12 out of 20 first trial responses observed in TA during standing (Misiaszek et al. 2016). In trials 2-10, responses were evoked in TA 55 out of 90 trials, which is significantly different (Fisher's Exact Test <0.001) from the 0 responses observed from 180 trials during standing. First trial responses in AD during treadmill walking occurred in 2 out of 10 participants, which is not significantly different (Fisher's Exact Test = 0.24) from the 10 out of 20 participants that responded to the first trial with AD during standing (Misiaszek et al. 2016). Responses in AD were rarely observed in trials 2-10 during treadmill walking with only 12 of 90 trials exhibiting a response. This is significantly less than (Fisher's Exact Test < 0.001) the 133 responses observed in 180 trials during standing.

Figure 3 depicts the occurrence of responses evoked following backward touch displacements. First trial responses were observed in SOL in 3 out of 10 participants during walking, which is not different from the 1 out of 5 responses observed during standing (Fisher's Exact Test = 1). Responses were evoked in 61 out of the 90 subsequent trials (trials 2-10) in SOL, with all participants responding in at least 4 of the remaining 9 trials which is significantly different from the 0 responses observed in 40 subsequent trials during standing (Fisher's Exact Test <0.001). First trial responses were observed in PD in 4 out of 10 participants during walking, which is not different from the 1 out of 5 participants that responded during standing (Fisher's Exact Test = 0.60). PD responded frequently in trials 2-10 with all 10 participants responding in at least 2 of the remaining 9 trials, for a total of 52 out of 90 trials. This was not different from the 26 responses observed in 40 subsequent trials during standing (Fisher's Exact Test = 0.56). [Trial 2-10 data were not reported for backward displacements during standing in Misiaszek et al. (2016), but are derived from the dataset obtained for that study.]

EMG response characteristics

Figure 4 depicts TA responses evoked following forward touch displacements for one participant (Participant 1). This participant responded with the first trial and in 6 of the subsequent 9 trials. The onset latency of the responses in this participant varied between 99.50 ms and 179.25 ms, however there did not appear to be a progressive or systematic change in either the onset latency or appearance of the responses with repeated exposures. The overall average onset latency across all 62 trials (across all participants) for which a response in TA was evoked was 144.4 (±37.1) ms, with onset latencies ranging between 67 ms and 192 ms. To evaluate if response latencies changed with repeated trials, the average latency of the first response observed (α) compared to the last response observed (ω) in each participant. As shown in Fig. 5A, the average latency of the α response was 133.1 (±39.1) ms, which was not significantly different from the average ω response latency of 136.2 (±43.9) ms (paired $t_{(9)}$ = 0.15, p=0.89). Response amplitudes (Fig. 5A) also did not systematically vary across trials with an average amplitude of the α response of 42.0 (±25.1) %MVC, compared with an average ω response amplitude of 34.4 (±29.8) %MVC (paired $t_{(9)}$=0.57, p=0.59).

The average response latency in SOL across all 64 responses to backward touch displacements was 123.7 (±34.1) ms, with onset latencies ranging between 52.25 ms and 194.75 ms. The average latency of the α response was 125.7 (±46.7) ms, which was not significantly different from the average ω response latency of 128.4 (±40.6) ms (paired $t_{(9)}$=0.23, p=0.82; Figure 5B). The average amplitude of the α response was 55.1 (±37.8) %MVC, which was not significantly different from the average amplitude of the ω response of 39.0 (±35.3) %MVC (paired $t_{(9)}$=1.58, p=0.15). The average response latency in PD across all 54 responses to backward touch displacements was 120.2 (±38.8) ms, with onset latencies ranging between 49.25 ms and 193.25 ms. The average latency of the α response was 110.7 (±44.8) ms, which was not significantly different from the average ω response latency of 120.5 (±45.7) ms (paired $t_{(9)}$=0.53, p=0.60; Figure 5B). The average amplitude of the α response was 8.7 (±13.1) %MVC, which was not significantly different from the average amplitude of the ω response of 14.2 (±25.9) %MVC (paired $t_{(9)}$=1.33, p=0.22).

Effects on the step cycle

Unexpected displacement of the light touch reference produced subtle changes in the ongoing stepping pattern of the participants. Figure 1B depicts the force sensitive resistor traces, along with ankle goniometer traces, for 1 trial from 1 participant. This example data suggests that in this trial, the forward touch displacement resulted in a small decrease in step cycle duration due to an early termination of the swing phase. The behavioural effects of the touch displacement appear to be quite small. Indeed, none of the participants lost their balance, stumbled or produced any other overt behaviours that would suggest the touch displacement presented a significant challenge to their continued walking. Nevertheless, displacement of the touch reference did result in significant changes to the stepping patterns.

Figure 6 depicts average step cycle, stance and swing durations across participants that received forward touch displacements. One-way repeated measures ANOVAs comparing control, trial 1 and trial 10 steps revealed main effect of trial on the duration of all three measures for the right leg (step cycle: $F_{(2,18)}$=10.49, p<0.001; stance: $F_{(2,18)}$=8.49, p<0.01; swing: $F_{(2,18)}$=9.78. p<0.01). Bonferroni post-hoc comparisons identified that the step cycle duration following the first touch displacement (1103.0 ± 120.2 ms) was significantly ($t_{(9)}$=4.04, p<0.01) shorter than the control steps (1169.1 ± 112.5 ms). Following the 10th touch displacement the step cycle duration was 1169.9 (± 127.2) ms, which was not different from the control steps ($t_{(9)}$=0.06, p=0.95). Stance durations following the first trial (677.4 ± 87.7 ms) were not significantly ($t_{(9)}$=1.19, p=0.26) different from control (690.4 ± 78.8ms). In contrast, the stance durations following trial 10 were 720.6 (± 89.7) ms, significantly longer than the control stance durations ($t_{(9)}$=2.99, p=0.015). First trial swing durations (425.6 ± 49.8 ms) were significantly reduced ($t_{(9)}$=3.78, p<0.01) compared to control (478.6 ± 70.4 ms). The trial 10 swing duration (449.3 ± 49.4 ms) was shorter than control, but not significantly at the adjusted α of 0.017 ($t_{(9)}$=2.58, p=0.03). No main effects of trial on the step cycle, stance or swing durations of the left leg were identified (step cycle: $F_{(2,18)}$=0.18, p=0.84; stance: $F_{(2,18)}$=0.73, p=0.50; swing: $F_{(2,18)}$=0.22, p=0.81).

Backward touch displacements did not result in any differences in the step parameters of either the right (step cycle: $F_{(2,18)}$=1.67, p=0.21; stance: $F_{(2,18)}$=2.35, p=0.12; swing: $F_{(2,18)}$=0.15, p=0.86) or left leg (step cycle: $F_{(2,18)}$=0.87, p=0.43; stance: $F_{(2,18)}$=1.95, p=0.17; swing: $F_{(2,18)}$=0.33, p=0.71).

Background EMG and touch force

Forward touch displacements did not result in systematic changes in the background EMG of any muscle recorded. Background activity in TA tended to be larger for trial 10 (24.3 ± 13.8 %MVC) than for trial 1 (18.6 ± 5.0 %MVC), but this was not significantly different ($t_{(9)}$=1.53, p=0.17). Similarly, backward touch displacements did not result in systematic changes in the background EMG of any muscle recorded. Background activity in SOL tended to be smaller for trial 10 (15.4 ± 12.9 %MVC) than for trial 1 (20.5 ± 12.5 %MVC), but the difference was not significant ($t_{(9)}$=1.02, p=0.34).

The vertical touch force applied by participants that received forward touch displacements was stable throughout the testing. The first trial touch force (0.76 ± 0.49 N) and the trial 10 touch force (0.75 ± 0.31 N) were not different ($t_{(9)}$=0.14, p=0.89). The touch force applied by participants that received backward touch displacements tended to decrease with repeated touch displacements [trial 1: 0.67 ± 0.31 N; trial 10: 0.56 ± 0.32 N], however this difference did not reach significance ($t_{(9)}$=1.70, p=0.12).

Psychophysical Outcomes

Fifteen participants (7 that received forwards touch displacements) completed the post-experiment questionnaire. The first question asked participants if they became aware that disturbances were being applied during the testing trial. Subsequent questions asked participants to detail the characteristics of any perturbations they experienced, including to estimate the number and source of any disturbances. The salient data are summarized in Table 1. Of the 15 participants that responded to the questionnaire, all but 1 reported detecting the presence of perturbations. Of the 14 that indicated they detected perturbations, 9 underestimated the total number of disturbances applied, 3 indicated the correct number, and 2 overestimated the number of perturbations. A total of 12 participants reported detecting the touch plate move, however only 5 participants identified that the disturbances were isolated to the touch plate. Nine participants indicated they felt that the treadmill belt speed had been disturbed, including 2 participants that identified that the disturbances were exclusively changes to the treadmill speed. Three participants reported being pushed or pulled during the testing. Seven participants reported a combination of disturbance sources. Participants that reported multiple sources of stimuli indicated that the touch plate disturbances occurred later in the trial. From these data it is apparent that the displacement of the touch plate was often misattributed to a gait disturbance or not perceived against the regular oscillation of the finger against the touch plate during walking. A sample of the written comments provided by the participants is also presented in Table 1.

Discussion

The aim of this study was to determine whether unexpected displacement of a light touch reference would evoke short-latency (<200 ms) responses in the ankle muscles during treadmill walking in the absence of vision. Indeed, responses in ankle muscles were observed in all 20 participants. It was further hypothesized that the challenge of walking on a treadmill without visual feedback would increase the importance of the light touch cues as a spatial reference, which would result in these responses being expressed more frequently than what was observed previously during standing. This second hypothesis is only partially supported. The number of participants that responded to the first unexpected displacement of the touch plate during walking was comparable to that observed during standing (Misiaszek et al. 2016). However, the persistent expression of responses on subsequent exposures to the touch plate displacement during treadmill walking was dramatically different from standing wherein responses were only ever observed in the ankle muscles with the first trial (Misiaszek et al. 2016).

First trial responses

Unexpected displacement of a light touch reference evokes postural responses in the ankle muscles of participants standing on a firm surface in approximately 60% of forward touch displacements, and 20% of backward touch displacements (Misiaszek et al. 2016). It was hypothesized that increasing the relevance of the touch reference, in this case by asking participants to walk on a treadmill without visual feedback, would increase the occurrence responses in the first trial as it was previously demonstrated that light touch provides an essential spatial reference in the absence of vision (Dickstein and Laufer 2004). However, this did not occur as responses were only evoked in 70% and 30% of first trials for forward and backward touch displacements, respectively. Similarly, it was recently shown that increasing the challenge to standing balance, by asking participants to stand on foam, did not affect the frequency with which first trial responses were observed following touch displacement with only 60% of participants responding to the first forward touch reference displacement (Misiaszek and Vander Meulen 2017). Together, these results suggests that the incorporation of tactile feedback for the control of stability may depend in part on the individual differences in the interpretation of the feedback. That is, if participants believe the touch reference is stable then presumably displacement of the touch plate is interpreted as displacement of the body relative to the touch plate and a postural response is generated. In contrast, some participants might anticipate that the touch plate could move and interpret the detected slip at the finger for what it is and respond with a different strategy, or not at all.

The first trial responses that were observed in this study are likely postural responses associated with a perceived balance disturbance. During standing, whether on a firm (Misiaszek et al. 2016) or foam (Misiaszek and Vander Meulen 2017) surface, the first trial responses in TA or SOL typically generate an anterior-posterior sway observed in the center of pressure. In the present study, the initial forward touch displacements at right heel-strike resulted in a significant reduction in the right step cycle duration, suggesting that the evoked response was functionally related to stabilizing gait. The initial backward touch displacements did not generate a similar adaptation to the step cycle, perhaps because only 3 participants responded to the backward touch displacement with a response in SOL. The most compelling evidence suggesting that the touch plate displacements were perceived as balance disturbances is the frequency with which participants reported believing the treadmill belt had changed speeds, or that the participant had received a pull at the waist. Although it is clear that the reported perceptions of the participants (Table 1) do not directly match the occurrence of responses in TA and SOL (Figure 2 and 3), the misinterpretation of the sensation from the fingertip indicates that in some participants the touch reference is expected to be stable. It is therefore reasonable to suggest that the sensorimotor set (Prochazka 1989), or motor system bias, would also be influenced by this expectation and the slip detected at the fingertip would trigger a correction to a presumptive "fall", or misstep.

The first exposure to a balance threat is normally the only exposure that an individual will experience. We are not often provided with the opportunity to learn from repeated exposures to balance threats. Despite this, the postural reaction generated must be sufficient to prevent a fall, or at least minimize the consequences of an impending fall. Allum et al. (2011) argue that due to the unexpected nature of balance disturbances they are often startling experiences. Therefore, it is possible that the first trial responses observed in our study are startle responses. Indeed, Campbell et al. (2013) argue that postural reactions include a startle component. Although startle likely contributes to the expression of the first trial response, the response is unlikely to be exclusively the result of startle. A common feature of first trial postural responses is habituation of the responses with repeated exposure to identical disturbances (Siegmund et al. 2008; Allum et al. 2011; Campbell et al. 2013). In our study, we did not see habituation of the responses as TA responses to forward displacements continued to be expressed at about the same frequency and SOL responses to backward displacements tended to increase in frequency with repeated exposure. Moreover, the amplitudes and latencies of the evoked responses in the ankle muscles were unaltered with repeated trials. Startle also typically evokes responses in SCM, including when the startle is induced by a balance disturbance (Oude Nijhuis et al. 2010; Campbell et al. 2013). In our study, responses in SCM were rarely observed and never with the first trial. Taken together, we argue that the responses observed here are not solely the result of a startle response, but represent a reaction to a presumptive balance disturbance initiated by the displacement of the finger relative to the position of the touch reference.

Trials 2-10

The most striking outcome of this study was the persistent expression of responses in the ankle muscles with repeated exposure to the touch plate displacements. This is in direct contrast to the absence of any responses observed by Misiaszek et al. (2016) when standing on a firm surface. Misiaszek and Vander Meulen (2017) also recently demonstrated continued expression of ankle muscle responses to touch plate displacements when standing on an unstable foam surface, suggesting that perhaps an increase threat to balance contributes to a more persistent expression of ankle muscle responses. However, another important difference between the responses observed on subsequent trials during walking and those during standing is the lack of the emergence of an obvious “arm-tracking” behaviour in the present study. During standing, whether on a firm surface (Misiaszek et al. 2016) or unstable foam surface (Misiaszek and Vander Meulen 2017), subsequent exposures of the touch plate displacement result in the extinction of a postural sway response observed in the center of pressure and the appearance of a distinct “arm-tracking” response wherein, following forward displacements, AD is activated and the elbow is extended. This did not occur in the present study, in particular for forward touch displacements where AD was rarely activated. Although backward touch displacements generated frequent responses in PD with subsequent trials during walking, this was not accompanied by any observable elbow flexion behaviour. Therefore, the distinct “arm-tracking” behaviour that emerged during standing did not occur during walking. This suggests that the responses observed with subsequent trials during walking continued to serve the same purpose as the responses to the first trial. However, this does not appear to be the case either as the step cycle was shorter following the first forward trial, as a result of a shorter swing phase, but not so for the tenth trial. On the contrary, the stance phase was prolonged following the tenth forward trial. Therefore, although responses in TA were more consistently expressed with repeated forward touch displacements during walking, it seems unlikely that the responses serve a consistent purpose with repeated trials.

Supporting the argument that the responses in TA during later trials do not likely serve the same purpose as the first trial response is the apparent emergence of a more consistent expression of responses in SOL following backward displacements of the touch plate (Fig. 3). These responses in SOL were not accompanied by any identifiable effects on the step cycle or related expression of responses in the other muscles tested. This evolution of a more consistent expression of responses in SOL with repeated trials is suggestive of a learned response to the touch plate displacement that perhaps allows the participant's position on the treadmill to be realigned with the new location of the touch reference. However, the functional relevance of the expression of the responses in the ankle muscles in trials 2-10 during treadmill walking is not easily delineated from the limited number of muscles recorded here and the minimal impact observed on the overall gait cycle. Nevertheless, it is apparent that the ankle muscles continued to be activated on subsequent trials and that these responses must be integrated within the ongoing task of treadmill locomotion.

Neural Mechanisms

The displacement of the touch reference beneath the finger resulted in a slip of the touch plate relative to the finger. The displacement of the touch plate did not result in a demonstrable disturbance in the elbow goniometer trace, suggesting the touch plate disturbance did not result in a physical disturbance to the posture of the arm. Therefore, any responses to the displacement of the touch plate are unlikely to be related to muscle stretch reflexes or other proprioceptor-related feedback from the arm. Muscle receptors from the intrinsic muscles of the hands or wrist muscles cannot be ruled out (Marchand-Pauvert et al. 2000) as it is possible the touch plate displacement produced movement at the finger joints or the onset of the touch plate movement initiated vibration. Nevertheless, tactile information from the fingertip is likely a strong candidate to detect the slip between the finger and the contact surface of the touch plate. Low-threshold mechanoreceptors of the skin are well suited for detecting slip with a contact surface. Srinivasan et al. (1990) demonstrated that slip stimuli at the fingerpad specifically activate slowly adapting (SA) mechanoreceptors with a clear directional bias. Ruffini endings (SAII-type receptors) are known to be sensitive to skin stretch and have been argued to be important in the direction-specific detection of slip of grasped objects (Abraira and Ginty 2013). Therefore, these receptors could also be important for signalling the direction-specific responses to the slip observed in this study. Other cutaneous receptors, including rapidly adapting type I mechanoreceptors (Meissner corpuscles) and Pacinian corpuscles are well-suited for detection of slip onset, but are less capable of coding the direction of slip (Srinivasan et al. 1990; Abraira and Ginty 2013).

Electrical stimulation of the median nerve at the wrist will excite large diameter afferents, including those that serve the Ruffini endings, Meissner corpuscles and Pacinian corpuscles of the fingerpad. Electrical stimulation of the median nerve leads to interlimb reflexes in the legs, indicating that the neural pathways necessary to link the cutaneous feedback from the fingertip with the ankle musculature are available (Delwaide and Crenna 1984). Therefore, it is possible the activation of cutaneous mechanoreceptors at the fingertip can directly influence the activity of muscles at the ankles related to postural control. Zehr and Duysens (2004) argue that these interlimb connections might be particularly relevant in coordinating the actions of the arms and legs in response to unexpected disturbances, especially during rhythmic quadrupedal activities such as walking. This speculation was supported recently by the findings of Forero and Misiaszek (2015) who demonstrated that interlimb cutaneous reflexes in ankle muscles, arising from median nerve stimulation, were facilitated when fingertip touch was used to stabilize walking on a treadmill with eyes closed. Median nerve interlimb reflexes have onset latencies typically ranging between 50 to 100 ms (Kagamihara et al. 2003), shorter than the 130 ms average onset latencies described presently. However, electrically evoked reflexes result from a large synchronous afferent volley, whereas the mechanical stimulus utilized here will produce asynchronous activation of afferents by first activating the mechanoreceptor. Delays related to the mechanosensory activation, integration of the asynchronous activity at central synapses, and within the noisier background of the walking task would all contribute to a response that is slower than the electrical analog. With some participants exhibiting evoked responses as early as 67 ms in TA or 52.25 ms in SOL following the touch displacement, the responses are sufficiently fast to suggest that spinal reflex circuitries could be involved. We therefore suggest that at least a portion of the responses evoked by these touch plate displacements arises from activation of interlimb cutaneous reflex pathways following the mechanical activation of cutaneous mechanoreceptors at the finger.

Limitations

During standing, the evoked responses had onset latencies of about 100 ms (Misiaszek et al. 2016; Misiaszek and Vander Meulen 2017). The responses observed here during walking were typically slower, with onset latencies of about 130 ms. Therefore, it is possible the responses evoked during walking represent different motor responses and the continued expression observed here is unrelated to increasing the balance threat by walking on a treadmill with eyes closed. Two factors might contribute to an increased onset latency for responses observed during walking. First, during treadmill walking the finger will oscillate on the surface of the touch plate with the rhythmic fore-aft motion of the body on the treadmill. This will create background levels of activity in the tactile receptors at the fingertip, potentially introducing background "noise" into the sensory system. The onset of the touch plate disturbance would then potentially be masked in part by this background noise. Indeed, the post experiment questionnaire completed by the participants indicates that most participants had difficulty identifying the number of displacements that were delivered. Second, the methods used to identify a response in the EMG traces utilize a 95% confidence band constructed from the control steps preceding the perturbation. The variability around these control steps will be larger than the variability in background activity that would occur during standing, potentially masking or delaying the detection of a change in the EMG activity. Therefore, the delay in the responses during walking is not likely reflective of differences in mediating neural pathways, but in technical aspects of the execution of the study.

In this study we used Fisher's Exact Tests to compare the frequency of response occurrences between treadmill walking and standing, utilizing data from Misiaszek et al. (2016) for comparison. Fisher's Exact Test allows for comparisons with low sample sizes and is preferred to other tests such as chi square tests, which require large sample sizes. However, Fisher's Exact Test is considered to be conservative and in our study, the comparison data for backward touch displacements during standing was a very small sample of only 5 participants. Therefore, there is a risk of committing a Type II error. Nevertheless, this does not present a major limitation for the current study as the *a priori* expectation was that the threat posed by walking on the treadmill with eyes closed would produce a critical reliance on the touch reference and result in a highly reliable expression of responses in TA or SOL, particularly on the first, unexpected trial. This clearly was not the case with our without the use of a statistical test.

The post experiment questionnaire used in this study was not tested for its psychometric properties. A particular risk with the execution of this questionnaire was the threat of recall bias as by the time the experiment was complete most participants had become aware that the test trial included some sort of disturbance. Recall bias might have contributed to the inaccurate estimation of the number of disturbances some participants experienced. Nevertheless, the questionnaire did yield useful insight into the experiences of the participants that suggests that the stimulus provided by the touch plate displacement was often misinterpreted as a balance or gait disturbance.

Functional Considerations

It is well established that light touch influences standing balance. Sway is stabilized when lightly touching a stable reference (Holden et al. 1994; Jeka and Lackner 1994), and becomes entrained to a contact surface that slowly oscillates (Jeka et al. 1998; Wing et al. 2011; Misiaszek et al. 2016). Moreover, rapid unexpected displacement of a light touch reference is capable of inducing a balance correction during standing, at least on the first trial (Misiaszek et al. 2016; Misiaszek and Vander Meulen 2017). Similarly, light touch during walking has been shown to stabilize the position of the body on a moving treadmill (Dickstein and Laufer 2004; Forero and Misiaszek 2013). In the present study, it was shown that rapid unexpected displacement of the touch reference is capable of inducing a response comparable to a balance response during treadmill walking. Together these results imply that the light touch sensory cues are incorporated in the balance control system to assist in regulating stability during both standing and walking.

Although light touch displacement evoked responses the ankle muscles during treadmill walking, the impact on the walking cycle was relatively small. Indeed, none of the participants stumbled, tripped or otherwise had difficulty continuing to walk on the treadmill following the touch displacement. Presumably, this is because the displacement used (12.5 mm) was relatively small and the participants were able to maintain contact with the touch plate thereby continuing to provide a spatial reference. The size of the touch plate was known to the participants as they had opportunity to see it during the earlier conditions. Therefore, the relative threat posed by the perceived perturbation would have been readily accounted for. Despite this, the disturbance was not simply ignored and responses in the ankle muscles were evoked, that did have impact on the timing of the step cycle. This indicates that tactile feedback from the hands could provide the earliest cue indicating a potential threat to balance if the threat is initiated at the hands or if the hands are being used for additional support. For example, Forero and Misiaszek (2014) showed that when a set of handles that are used to stabilize subjects walking on a treadmill are unexpectedly moved, rapid responses are triggered in the legs to restore balance. Tactile sensations from the hands would provide a logical trigger for the responses observed. This could have important implications for understanding balance control for individuals that use mobility aids and assistive devices during walking where the threat to stability could be detected through the interface with the external support.

It is also important to note, however, that the touch plate displacement used in this study did not create an actual mechanical disturbance to the balance of the individual. Despite this, participants generated responses in the ankle muscles and adapted their step cycles. In other words, the participants reacted with a “false-positive” reaction that could itself be the cause of a potential fall or misstep. Similar sensory illusions influencing balance have been demonstrated with vestibular (Day et al. 2002), visual (van Asten et al. 1988), and muscle mechanoreceptor inputs (Hayashi et al. 1981). These sorts of sensory illusions are potentially destabilizing in themselves, and could pose a particular threat for individuals with compromised balance control. The difference between interpreting a slip at the finger as the body moving relative to a spatial reference versus the movement of the object relative to the body could profoundly affect the consequences of that event, particularly during a complex task such as walking.

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Figure Legends

Figure 1: A) Schematic diagram of the experimental set-up. Participants walked on a motorized treadmill while wearing darkened goggles and lightly touching a touch plate. The touch plate was mounted on an acme screw driven by a stepper motor to produce linear fore-aft linear displacements. B) Data traces from one participant that received a forward touch plate displacement delivered at heel-strike. The thick traces depict a single data sweep for the step that included the touch displacement. The thin traces depict average control step data for the five steps preceding the disturbed step. The vertical dashed line is aligned to the onset of the touch plate displacement. The vertical scales for the EMG traces are expressed as % MVC. C) Sample subtracted EMG trace which were used to identify the presence and onset latency of evoked EMG responses. The thick trace depicts a single data sweep following subtraction of the average control step trace. The thin lines represent the 95% confidence band around the average control steps, which is set to zero having been subtracted from itself. The shaded area indicates the window used to analyze the response amplitude. TA – tibialis anterior; SOL – soleus; AD – anterior deltoid; FSR – force sensitive resistor (foot contact).

Figure 2: Grid indicating the presence of detectable EMG responses in TA, AD, VL, and BB following forward touch plate displacements delivered at heel strike across all trials and participants. The darkened cells indicate trials for which a response was evoked.

Figure 3: Grid indicating the presence of detectable EMG responses in SOL, PD, BF, and TB following backward touch plate displacements delivered at heel strike across all trials and participants. The darkened cells indicate trials for which a response was evoked.

Figure 4: Subtracted traces from one participant (participant #1) showing the EMG responses in TA for the 7 trials that generated a clear response to forward touch plate displacements. The vertical dashed lines indicate the onset of the evoked response in each trace.

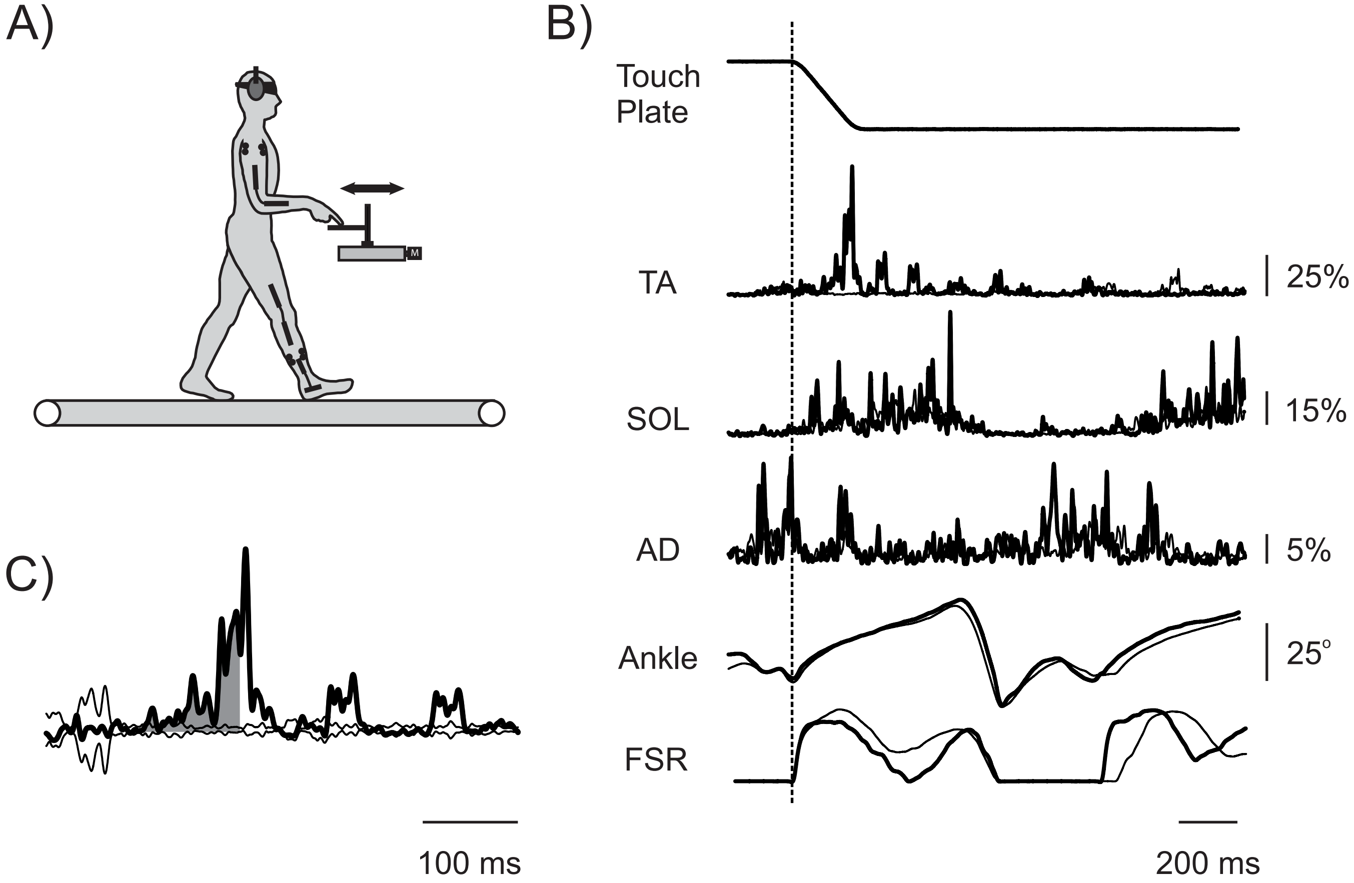
Figure 5: A) Onset latencies and amplitudes for the first response observed (α) and the last response observed (ω) in TA following forward touch displacements. B) Onset latencies and amplitudes for α and ω responses in SOL and PD following backward touch displacements.

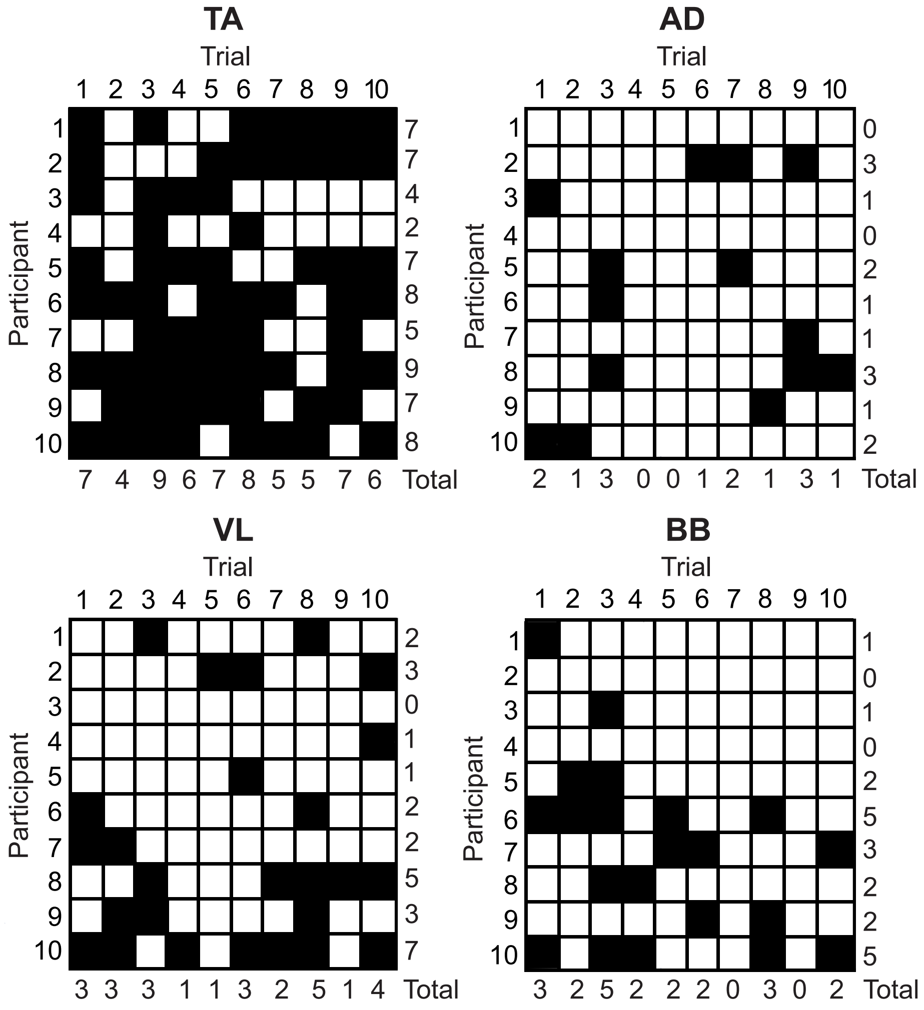
Open circles represent individual data points. Horizontal lines indicate the means with standard deviations.

Figure 6: Means and standard errors of the step Cycle, Stance and Swing durations for the right leg from Control, Trial 1 and Trial 10 steps for forward touch displacements. The overhead lines indicate significant differences identified by Bonferoni post-hoc comparisons. Note that the ordinate of each plot does not begin at zero.

Table 1: Psychophysical data obtained from a post-experiment questionnaire. The numbers in the cells indicate the number of times the participant perceived: a change in treadmill belt speed (Treadmill), a push or pull at the waist (Push/Pull), or displacement of the touch plate (Touch Plate). Comments provided by participants describing the experience are also presented.

	Participant No.	Event Perceived			Description of Experience
		Treadmill	Push/Pull	Touch Plate	
Forward	4	0	0	4	
	5	6	4	4	It felt like a quick stop or start of the treadmill
	6	0	0	10	I felt the touch plate move beneath my finger and my finger slip
	7	0	0	0	
	8	4	3	3	I felt jolted several times, like you shoved me
	9	8	0	8	I felt something, but wasn't sure if it was at my finger or at my feet
	10	4	2	1	
Backward	13	7	0	4	At times I felt jolts to my feet and other times the jolts were through my finger
	14	3	0	0	I felt the treadmill change speed
	15	0	0	10	I lost balance because my finger slipped and I started to walk funny
	16	4	0	5	I felt the treadmill pulse sometimes and the bar I was touching move sometimes
	17	0	0	7	I felt my fingertip moved
	18	0	0	9	I felt the metal plate bounce back once in a while
	19	1	0	1	
	20	5	0	0	I felt like brakes were applied to the treadmill


A)
M
B)
Touch Plate
TA
25%
SOL
15%
AD
5%
Ankle
25°
FSR
200 ms
C)
100 ms



TA

Trial

Participant	1	2	3	4	5	6	7	8	9	10	
1	■	□	■	□	□	■	■	■	■	■	7
2	■	□	□	□	■	■	■	■	■	■	7
3	■	□	■	■	■	□	□	□	□	□	4
4	□	□	■	□	□	■	□	□	□	□	2
5	■	□	■	■	■	□	□	■	■	■	7
6	■	■	■	□	■	■	■	□	■	■	8
7	□	□	■	■	■	■	□	□	■	□	5
8	■	■	■	■	■	■	■	□	■	■	9
9	□	■	■	■	■	■	□	■	■	□	7
10	■	■	■	■	□	■	■	■	□	■	8
	7	4	9	6	7	8	5	5	7	6	Total

AD

Trial

Participant	1	2	3	4	5	6	7	8	9	10	
1	□	□	□	□	□	□	□	□	□	□	0
2	□	□	□	□	□	■	■	□	■	□	3
3	■	□	□	□	□	□	□	□	□	□	1
4	□	□	□	□	□	□	□	□	□	□	0
5	□	□	■	□	□	□	■	□	□	□	2
6	□	□	■	□	□	□	□	□	□	□	1
7	□	□	□	□	□	□	□	□	■	□	1
8	□	□	■	□	□	□	□	□	■	■	3
9	□	□	□	□	□	□	□	■	□	□	1
10	■	■	□	□	□	□	□	□	□	□	2
	2	1	3	0	0	1	2	1	3	1	Total

VL

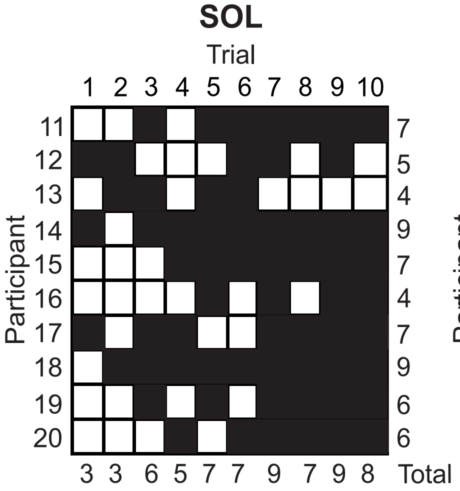
Trial

Participant	1	2	3	4	5	6	7	8	9	10	
1	□	□	■	□	□	□	□	■	□	□	2
2	□	□	□	□	■	■	□	□	□	■	3
3	□	□	□	□	□	□	□	□	□	□	0
4	□	□	□	□	□	□	□	□	□	■	1
5	□	□	□	□	□	■	□	□	□	□	1
6	■	□	□	□	□	□	□	■	□	□	2
7	■	■	□	□	□	□	□	□	□	□	2
8	□	□	■	□	□	□	■	■	■	■	5
9	□	■	■	□	□	□	□	■	□	□	3
10	■	■	□	■	□	■	■	■	□	■	7
	3	3	3	1	1	3	2	5	1	4	Total

BB

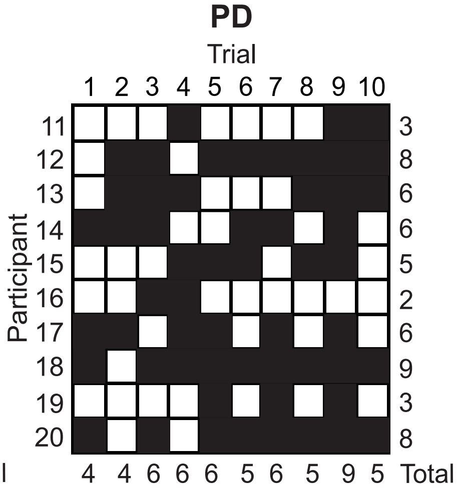
Trial

Participant	1	2	3	4	5	6	7	8	9	10	
1	■	□	□	□	□	□	□	□	□	□	1
2	□	□	□	□	□	□	□	□	□	□	0
3	□	□	■	□	□	□	□	□	□	□	1
4	□	□	□	□	□	□	□	□	□	□	0
5	□	■	■	□	□	□	□	□	□	□	2
6	■	■	■	□	■	□	□	■	□	□	5
7	□	□	□	□	■	■	□	□	□	■	3
8	□	□	■	■	□	□	□	□	□	□	2
9	□	□	□	□	□	■	□	■	□	□	2
10	■	□	■	■	□	□	□	■	□	■	5
	3	2	5	2	2	2	0	3	0	2	Total



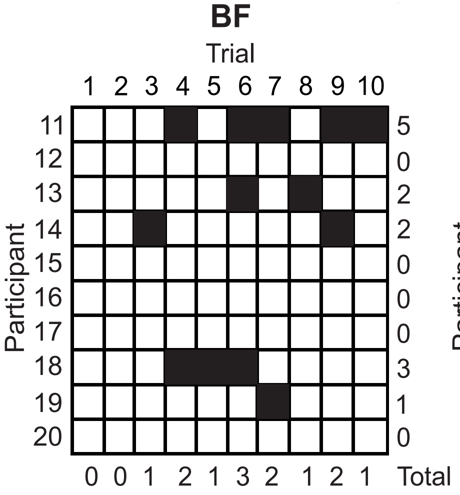
SOL

Participant	Trial										
	1	2	3	4	5	6	7	8	9	10	
11	□	□	■	□	■	■	■	■	■	■	7
12	■	■	□	□	□	■	■	□	■	□	5
13	□	■	■	□	■	■	□	□	□	□	4
14	■	□	■	■	■	■	■	■	■	■	9
15	□	□	□	■	■	■	■	■	■	■	7
16	□	□	□	□	■	□	■	□	■	■	4
17	■	□	■	■	□	□	■	■	■	■	7
18	□	■	■	■	■	■	■	■	■	■	9
19	□	□	■	□	■	□	■	■	■	■	6
20	□	□	□	■	□	■	■	■	■	■	6
	3	3	6	5	7	7	9	7	9	8	Total



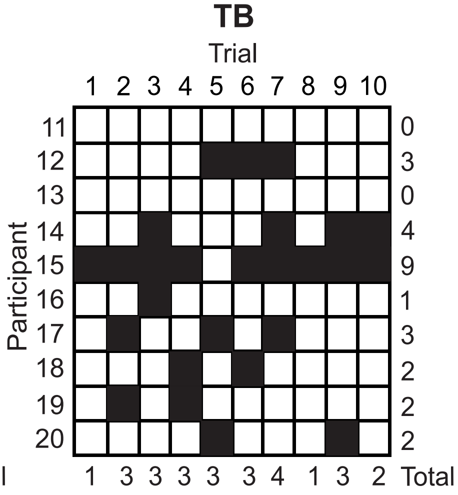
PD

Participant	Trial										
	1	2	3	4	5	6	7	8	9	10	
11	□	□	□	■	□	□	□	□	■	■	3
12	□	■	■	□	■	■	■	■	■	■	8
13	□	■	■	■	□	□	□	■	■	■	6
14	■	■	■	□	□	■	■	□	■	□	6
15	□	□	□	■	■	■	□	■	■	□	5
16	□	□	■	■	□	□	□	□	□	□	2
17	■	■	□	■	■	□	■	□	■	□	6
18	■	□	■	■	■	■	■	■	■	■	9
19	□	□	□	□	■	□	■	□	■	□	3
20	■	□	■	□	■	■	■	■	■	■	8
	4	4	6	6	6	5	6	5	9	5	Total



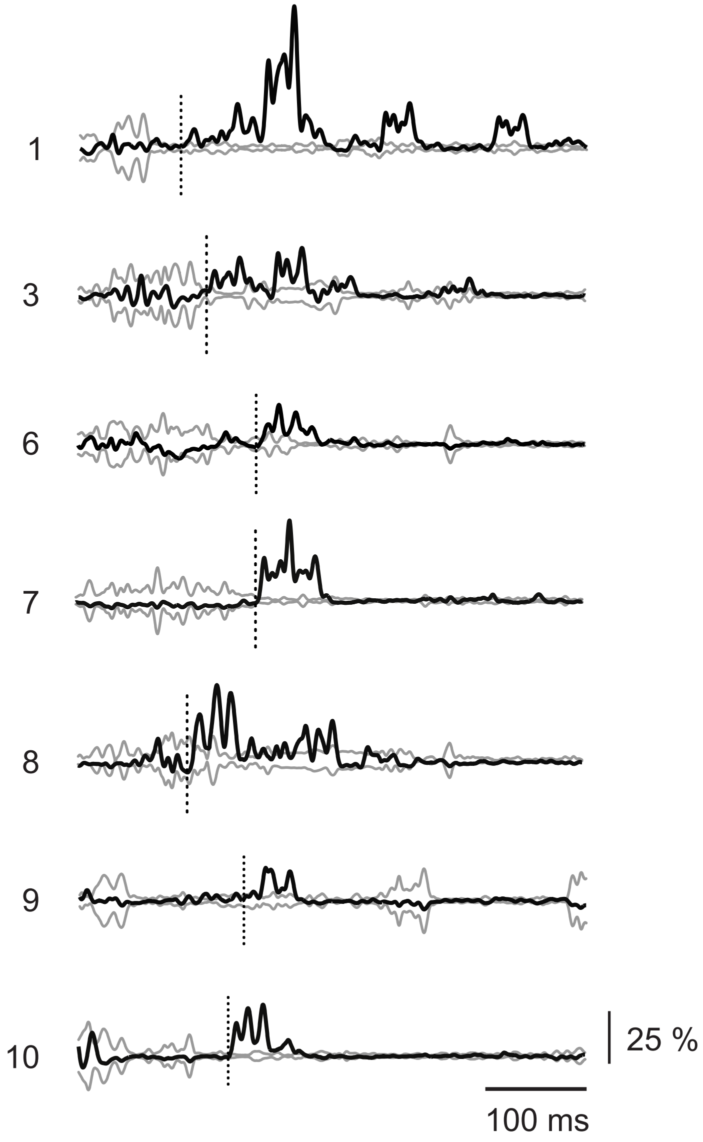
BF

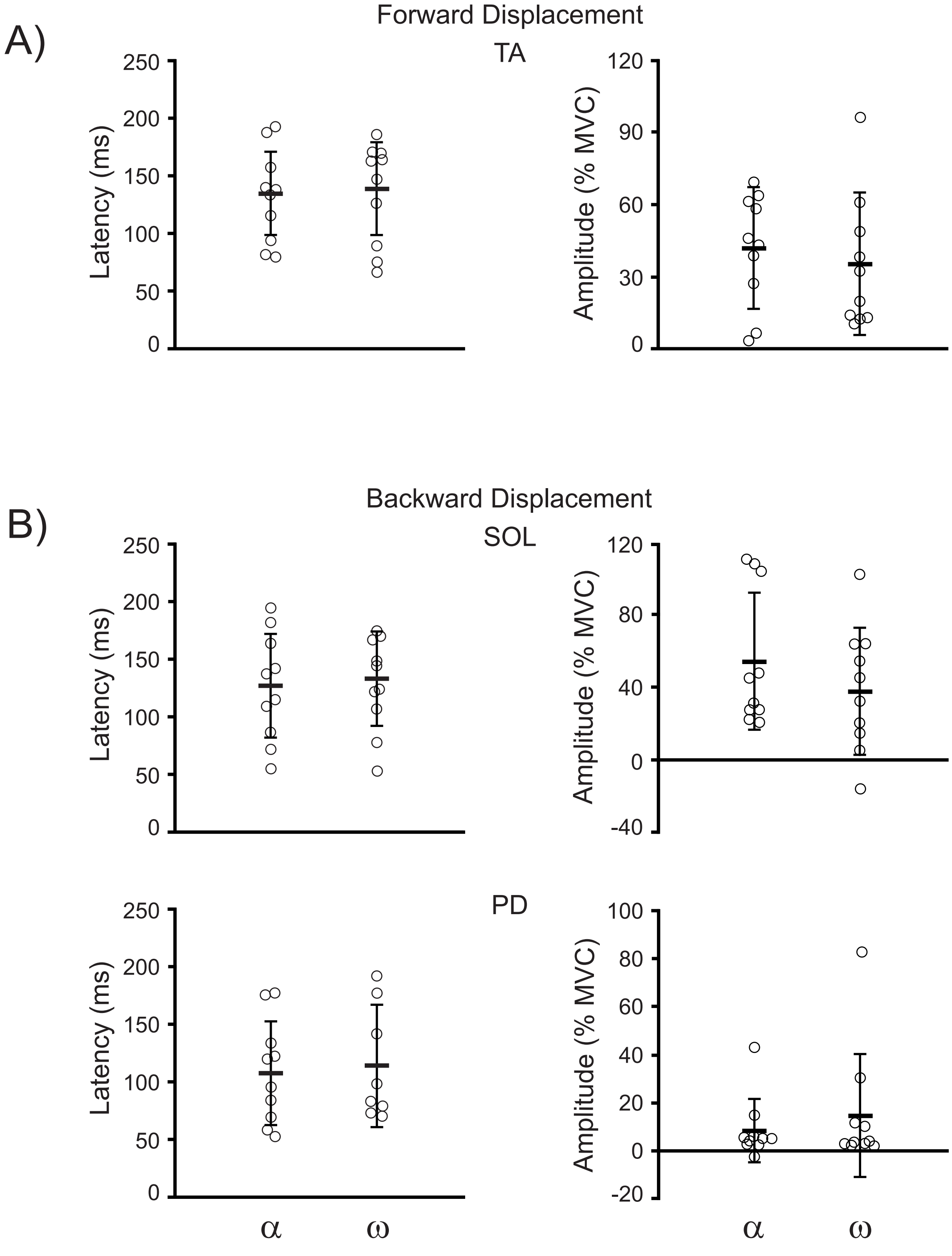
Participant	Trial										
	1	2	3	4	5	6	7	8	9	10	
11	□	□	□	■	□	■	■	□	■	■	5
12	□	□	□	□	□	□	□	□	□	□	0
13	□	□	□	□	□	■	□	■	□	□	2
14	□	□	■	□	□	□	□	□	■	□	2
15	□	□	□	□	□	□	□	□	□	□	0
16	□	□	□	□	□	□	□	□	□	□	0
17	□	□	□	□	□	□	□	□	□	□	0
18	□	□	□	■	■	■	□	□	□	□	3
19	□	□	□	□	□	□	■	□	□	□	1
20	□	□	□	□	□	□	□	□	□	□	0
	0	0	1	2	1	3	2	1	2	1	Total

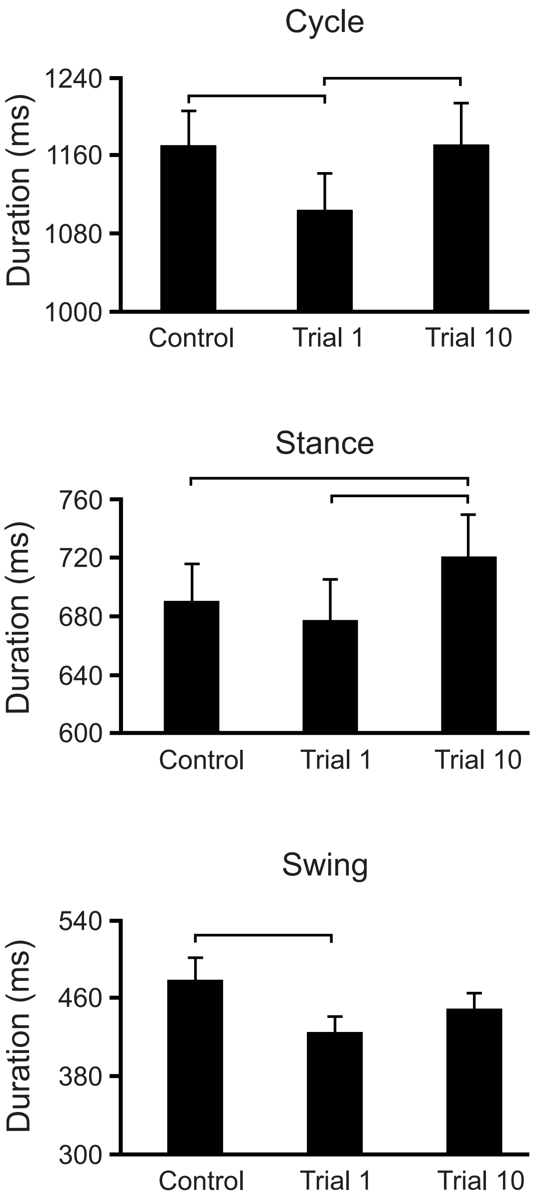


TB

Participant	Trial										
	1	2	3	4	5	6	7	8	9	10	
11	□	□	□	□	□	□	□	□	□	□	0
12	□	□	□	□	■	■	■	□	□	□	3
13	□	□	□	□	□	□	□	□	□	□	0
14	□	□	■	□	□	□	■	□	■	■	4
15	■	■	■	■	□	■	■	■	■	■	9
16	□	□	■	□	□	□	□	□	□	□	1
17	□	■	□	□	■	□	■	□	□	□	3
18	□	□	□	■	□	■	□	□	□	□	2
19	□	■	□	■	□	□	□	□	□	□	2
20	□	□	□	□	■	□	□	□	■	□	2
	1	3	3	3	3	3	4	1	3	2	Total


1
3
6
7
8
9
10
25 %
100 ms


A)
Forward Displacement
TA
Latency (ms)
250
200
150
100
50
0
Amplitude (% MVC)
120
90
60
30
0
B)
Backward Displacement
SOL
Latency (ms)
250
200
150
100
50
0
Amplitude (% MVC)
120
80
40
0
-40
PD
Latency (ms)
250
200
150
100
50
0
Amplitude (% MVC)
100
80
60
40
20
0
-20
α
ω
α
ω



Cycle
Duration (ms)
1240
1160
1080
1000
Control
Trial 1
Trial 10
Stance
Duration (ms)
760
720
680
640
600
Control
Trial 1
Trial 10
Swing
Duration (ms)
540
460
380
300
Control
Trial 1
Trial 10