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# Anticipation of direction and time of perturbation modulates the onset latency of trunk muscle responses during sitting perturbations

## 1. Introduction

The neuromuscular system of the trunk is mainly responsible for maintaining trunk stability during sitting and standing (Preuss and Fung, 2008). Muscle activations following disruption of quiet sitting (Masani et al., 2009; Milosevic et al., 2012; Preuss and Fung, 2008; Shahvarpour et al., 2015) and standing (Carpenter et al., 2008; Cresswell et al., 1994; Preuss and Fung, 2008; Stokes et al., 2000; Wilder et al,. 1996) have previously been studied with the objective to better understand the neural mechanisms responsible for trunk stability. Perturbations were delivered in the form of direct perturbation to the trunk (i.e., pushing or pulling of the trunk) (Masani et al., 2009; Milosevic et al., 2012; Shahvarpour et al., 2015; Stokes et al., 2000; Wilder et al., 1996) or by perturbing the surface on which the individual was sitting or standing (Carpenter et al., 2008; Preuss and Fung 2008). During such experiments, the type of perturbation (Carpenter et al., 2008), the direction of perturbation and the posture of the participant prior to the perturbation (i.e., sitting or standing posture) (Preuss and Fung, 2008) play a critical role in the response to the perturbation. The latencies of the trunk muscle activations with respect to the onset of perturbation were reported in the range between 24 - 55 ms (Cresswell et al., 1994) and 25 - 150 ms (Stokes et al., 2000) during standing trunk loading, and 100 ms - 200 ms during standing and 70 ms - 250 ms during sitting support surface translations (Preuss and Fung, 2008). Muscle response latencies in the range between 30 - 50 ms are generally classified as monosynaptic stretch reflexes (M1); 50 - 80 ms are classified as functional polysynaptic stretch reflexes (M2); 80 - 120 ms are classified as triggered reactions;

and 120 - 180 ms are classified as voluntary reactions (M3) (Schmidt, 2011; Wilder et al., 1996). Previously, it has been suggested that that the trunk neuromuscular system, in response to sudden perturbations, has short latency responses based on monosynaptic reflexes (Granata et al., 2004) or medium latency responses based simple polysynaptic reflexes (Stokes et al., 2000).

Complexity of the central nervous system control of the trunk is revealed in situations when perturbations can be anticipated. Anticipatory postural adjustments are often investigated during internal perturbations, and those studies revealed that anticipation can lead to stiffening of the joints and adjustment of the initial posture before the onset of rapid limb movements (Allison et al., 2003) or self-loading perturbations (Cresswell et al., 1994) since the subjects prepare for the upcoming perturbation. In case of external perturbations, such as those delivered by direct perturbations of the trunk or by perturbing the surface on which the subject is standing or sitting, neuromuscular responses can be studied with and without the anticipation of perturbation to investigate the effects of anticipating a perturbation. During such perturbations, there are two types of anticipation: i) spatial anticipation - which is the prediction of typo of perturbation or direction of perturbation; and ii) temporal anticipation - which is the prediction of the time of perturbation (Wilder et al., 1996). Wilder et al. (1996) reported that the trunk muscle onset response times were affected by temporal anticipation during standing balance, but they did not investigate the effects of spatial and temporal anticipation systematically. Others have reported increased trunk muscle (Aleksiev et al., 1996) and neck muscle (Kuramochi et al., 2004) activations when timing of the external perturbations could be anticipated. However, the effect of anticipation of the perturbation on the trunk neuromuscular responses during sitting is still not well understood. To our knowledge no study has investigated the effect of anticipation of direction and time of perturbation on the neuromuscular responses during sitting support surface translations. Therefore, a systematic investigation of the neuromuscular responses during sitting balance support surface translations, with and without anticipation of direction and time of the perturbation, is required.

We hypothesized that amplitude of the trunk muscle responses will be larger during anticipated perturbations compared to unanticipated perturbations. The objectives of this study were to identify the responses of the trunk muscles to sudden support surface translations during sitting and to quantify the effects of anticipation of direction of perturbation and time of perturbation on modulation of the trunk neuromuscular responses.

## 2. Methods

### *2.1. Participants*

Twelve healthy, male individuals participated in this study. The age, body mass and height of participants were 26.8 ± 3.3 years, 64.7 ± 7.8 kg, and 171.6 ± 7.8 cm (mean ± SD), respectively. None of the participants had history of neurological or musculoskeletal impairments. Informed consent was obtained from all individual participants included in the study in accordance with the principles of the Declaration of Helsinki. The experimental procedures were approved by the local institutional ethics committee.

### *2.2. Experimental Protocol*

Participants were seated on a kneeling chair and were instructed to maintain a relaxed upright posture of the trunk while keeping their arms crossed on their chest. Perturbations in the forward or backward direction were applied as support surface translations using an instrumented treadmill FIT (Bertec, USA). Perturbations were delivered with or without spatial and temporal cues (i.e., direction and time of perturbation, respectively) in the following conditions: i) both direction and time of the perturbation could not be anticipated ($D^{-} T^{-}$); ii) the direction could not be anticipated, but the time of the perturbation could be anticipated ($D^{-} T^{+}$); iii) the direction could be anticipated, but the time of perturbation could not be anticipated ($D^{+} T^{-}$); and iv) both direction and time of the perturbation could be anticipated ($D^{+} T^{+}$). In order to examine if the subjects contracted their trunk muscles before the perturbation when the perturbation could be anticipated or if the anticipation only affected the reactive responses, two catch trial conditions were also incorporated: v) the direction could not be anticipated and the time of perturbation could be anticipated, but the perturbation was not delivered ($Catch^{-}$); and vi) both direction and time of perturbation could be anticipated but the perturbation was not delivered ($Catch^{+}$). In total, 192 randomly ordered trials were recorded for each participant, including 16 repeated trials for each of the six conditions for the forward and backward perturbation direction (i.e., 16 trials x 6 conditions x 2 directions).

Before recording the experimental data, participants were given an opportunity to become familiarized with the experimental procedure. They were perturbed six times in different directions, and these data were not used in the analysis. This was done to ensure that the initial learning of a new task is not contaminating the experimental results.

To prevent fatigue, data was collected in four sessions (48 trials per session) with a 5 min break between sessions. Each of the four sessions lasted approximately 15 min. The session order was randomized between participants.

The direction of perturbation (i.e., spatial cue) was indicated to the participant prior to delivering perturbations using verbal instructions. During two of the four sessions participant could anticipate the perturbation direction. In these sessions, perturbations were always delivered as either forward or backward perturbations during the entire session. In the remaining two sessions, the perturbations were delivered in the forward and backward direction such that the participant could not anticipate which perturbation will be next.

The time of perturbation (i.e., temporal cue) was indicated to the participant in all four sessions, during the conditions with anticipated perturbation time, using an audio signal. The audio signal was a brief tone that occurred 1 - 3 sec before the perturbation, such that the participants would be ready for the perturbations but wouldn't use preparatory actions before the perturbation occurred. The triangle-shaped velocity perturbation was applied over a period of 120 ms. The resultant average perturbation displacement during all trials was 7.3 ± 0.3 cm and the peak acceleration was 12.3 ± 2.7 m/sec$^2$ (mean ± SD). The perturbations displacement and accelerations were equal across experimental conditions. After each perturbation was delivered, the treadmill was slowly returned to the starting position and the next perturbation trial was started after 5 - 7 sec, such that the participants could not anticipate the next perturbations.

### *2.3. Data Acquisition*

#### *2.3.1. Trunk Muscle Electromyography and Force Signal Measurements*

Trunk muscle activity was recorded using surface electromyography (EMG) unilaterally on the right side of the body, assuming that the participant has symmetric responses (Masani et al., 2009). Disposable EMG electrodes (Ag-AgCl) with 1 cm separation were placed between the electrodes on the abdominal muscles: rectus abdominis, 3 cm right and 1 cm superior to the umbilicus (RA-1) and rectus abdominis, 3 cm right and 1 cm inferior to the umbilicus (RA-2); as well as erector muscles: thoracic erector spinae, 5 cm right of the T9 spinous process (T9) and lumbar erector spinae, 3 cm right of the L3 spinous process (L3). A reference electrode was placed over the clavicle. These muscles were chosen because they contribute significantly to the anterior-posterior trunk stability (Masani et al., 2009; Milosevic et al., 2012). Data was acquired using a surface EMG system Bagnoli-8 (Delsys Inc., USA) with a pre-amplification gain of 1,000. The frequency response of the signal was between 20 and 450 Hz, which is in the range of the previous studies examining trunk muscle onset latencies during perturbations (Carpenter et al., 2008; Granata et al., 2004; Stokes et al., 2000) and effectively removes motion artifact during fast perturbations while preserving EMG signal energy (De Luca et al., 2010).

The anterior-posterior ground reaction force on the treadmill surface was also recorded using the instrumented treadmill FIT (Bertec, USA) to identify the exact start of the perturbation. All EMG data as well as the force outputs were recorded using a 12-bit data acquisition system NI6071E (National Instruments, USA) with 2,000 Hz sampling rate.

*2.3.2. Trunk Center of Mass Measurements*

Three-dimensional trunk kinematics were collected with 6 Oqus cameras (Qualisys Motion Capture Systems, Sweden), to assess postural performance of the upper body after perturbations. A total of 24 passive reflective markers were placed on the following upper body segments: i) head (to C7); ii) upper thoracic segment including arms (T1–T6); iii) lower thoracic segment (T7–T12); iv) lumbar trunk segment (L1–L5); and v) pelvis segment (Figure 1). A detailed description of the marker placements is described in Crosbie et al. (1997) and has subsequently been used by Preuss and Fung (2008) during sitting and standing perturbations. An additional marker was placed on the treadmill to record the perturbation platform position. All marker positions were recorded in the absolute coordinate frame at were sampled at 200 Hz using the Qualisys Track Manager Software (Qualisys Motion Capture Systems, Sweden). The head, thorax (i.e., combining the measured upper and lower thorax segments), abdomen and the pelvis segments were combined to obtain a single upper body segment, representing the trunk. The upper body center of mass (COM) in the anterior-posterior direction was calculated according the established methods described by Winter (2009).

### *2.4. Data Analysis*

For all trials, the start of the perturbation (t = 0) was defined as the time when the anterior-posterior force component on the treadmill exceeded 15 N.

#### *2.4.1. EMG Responses*

Only the primary muscle responses were examined in the EMG analysis in order to analyze how the central nervous system modulates the responses with anticipatory information. Perturbations were applied as forward or backward support surface translations, resulting in backward or forward trunk bending, respectively (Figure 2). Therefore, during forward perturbations (i.e., backward trunk bending), RA-1 and RA-2 muscle responses were analyzed and during backward perturbations (i.e., forward trunk bending) T9 and L3 muscle responses were analyzed. All EMG data were first rectified by taking the absolute value of the signal. Analysis of the EMG signals included computing: 1) the tonic muscle activity, which was defined as the root mean square of the EMG signal in the 50 ms window before the perturbation; 2) the onset time of the muscle response, which was automatically identified using the integrated protocol (IP) algorithm (Santello et. al., 1998; Allison 2003); and 3) phasic muscle activity, which was defined as the root mean square of EMG signal in the 100 ms window after the muscle onset.

*2.4.2. COM Responses*

The trunk COM responses were evaluated to characterize the movement of the upper body and evaluate postural performance. The trunk COM position was low-pass filtered at 50 Hz using a fourth-order, zero-phase-lag Butterworth filter. Analysis of the COM responses included calculating: 1) the trunk movement onset, which was determined using the IP algorithm (Santello et. al., 1998; Allison, 2003); 2) the trunk maximum displacement, which was determined as the maximum displacement of the COM relative to the chair (obtained by subtracting the chair position form the maximum trunk COM) in the 500 ms window after the perturbation; 3) the time to maximum displacement, which was the time it took the COM to reach the maximum displacement; 4) the trunk maximum velocity, which was determined as the maximum velocity of the COM in the 500 ms window after the perturbation; and 5) the time to maximum velocity, which was the time it took the COM to reach maximum velocity.

***2.5. Missing Data***

For EMG data during the experiment, 7% of trials for RA-1 muscle, 5% of trials for RA-2 muscle, 17% of trials for T9 muscle, and 11% of trials for L3 muscle were rejected when the muscle onset time was identified as an outlier and it was not possible to determine the onset of muscle activity due to excessive co-activation of muscles. Of those, 8% of trials for $D^- T^-$, 7% of trials for $D^- T^+$, 13% of trials for $D^+ T^-$, and 12% of trials for $D^+ T^+$ were rejected. For kinematics data, 9% of all data was rejected when the markers required to calculate the COM were missing and could not be interpolated during post processing.

### *2.6. Statistical Analysis*

Comparisons between experimental conditions for the EMG and COM analyses were performed using the one-way repeated measures analysis of variance (ANOVA) with Tukey post-hoc multiple comparisons when a significant difference was found on the ANOVA test. All selected measures were also tested using the Shapiro-Wilk test to identify if they were normally distributed. In cases where one of the measures was not normally distributed, a non-parametric, Kruskal Wallis test was used to confirm the ANOVA test. Significance level was set to $p$<0.05.

The catch trials (i.e., $Catch^-$ and $Catch^+$) were compared to the main experimental conditions (i.e., $D^- T^-$, $D^- T^+$, $D^+ T^-$ and $D^+ T^+$), and pairwise comparison between the catch trials and the corresponding experimental conditions (i.e., $Catch^-$ compared to $D^- T^-$ and $D^- T^+$, and $Catch^+$ compared to $D^+ T^-$ and $D^+ T^+$) was used to confirm these results, only for the analysis of the tonic muscle activity in order to ensure that muscles were not preloaded before the perturbations. Once this was confirmed, only the main experimental conditions were compared, as there was no phasic activity during the catch trials.

## 3. Results

An example of the EMG and COM data is shown in Figure 2. Illustrated are the typical responses following forward and backward perturbations for each experimental condition.

### *3.1. Trunk Muscle Responses*

#### *3.1.1. Tonic EMG Activity*

There were no differences in the tonic muscle activity between experimental conditions and catch trials for the RA-1 ($p$=0.533), RA-2 ($p$=0.366), T9 ($p$=0.204) and L3 ($p$=0.140) muscles (Table 1). This confirmed that the muscles were not preloaded differently between different experimental and catch conditions.

#### *3.1.2. EMG Onset Latency*

The onset times were significantly different between experimental conditions for RA-1 ($p$<0.001), RA-2 ($p$<0.001), T9 ($p$<0.001) and L3 ($p$<0.001) muscles (Table 1). Tukey post-hoc multiple comparisons indicated that when both direction and time of perturbation were anticipated, trunk muscle onset latencies were shorter for all muscles. Anticipation of the direction and the time of perturbation seem to both contribute to the shorter onset latencies (Table 1).

#### *3.1.3. Phasic EMG Activity*

There were no differences in the phasic muscle activity between experimental conditions for the RA-1 ($p$=0.612), RA-2 ($p$=0.700), and T9 ($p$=0.300) muscles, while there was a significant difference for L3 ($p$=0.005) (Table 1). Tukey post-hoc multiple comparisons indicated that there was a smaller phasic muscle activity in the L3 muscle only when both direction and time of perturbation were anticipated (Table 1).

### *3.2. Trunk Kinematics Responses*

*3.2.1. Onset of COM Movements*

There were no differences in the trunk movement onset time between experimental conditions for the forward perturbations ($p$=0.938) and backward perturbations ($p$=0.839) (Table 2). This confirmed that the subjects did not start moving the trunk differently between experimental conditions.

*3.2.2. Maximum COM Displacement*

There were no differences in the maximum trunk displacement between conditions for the forward perturbations ($p$=0.357) and backward perturbations ($p$=0.139). Also, the time to maximum displacement was not different between experimental conditions for the forward perturbations ($p$=0.973) and backward perturbations ($p$=0.711) (Table 2).

*3.2.3. Maximum COM Velocity*

There were no differences in the maximum trunk velocity between conditions for the forward perturbations ($p$=0.133) and backward perturbations ($p$=0.489). However, the time to maximum displacement was significantly different between experimental conditions for the forward perturbations ($p$=0.003) and backward perturbations ($p$=0.007) (Table 2). Tukey post-hoc multiple comparison analysis indicated that when both direction and time of perturbation were anticipated, the time required to reach the maximum trunk velocity was faster during both the forward and backward perturbations. Anticipation of the direction and the time of perturbation both seem to have contributed to this result slightly (Table 2).

# 4. Discussion

## *4.1. Trunk Response Latencies*

The average abdominal muscle response latencies in our study (i.e., RA-1 and RA-2) were in the range between 99.1 and 116.6 ms during forward perturbations and erector muscles response latencies (i.e., T9 and L3) between 90.2 and 117.4 ms during backward perturbations, while the onset of the trunk center of mass movement was on average 46.7 ms after the forward perturbations and 37.9 ms after the backward perturbations (i.e., approximately 40 ms after the perturbation). Effectively this suggests that trunk muscles activated approximately 60 ms after the movement of the trunk.

During postural responses to a perturbation, a number of phasic muscle responses occur to compensate for the perturbation (Schmidt, 2011). They include: short latency, monosynaptic stretch reflex (Ml) with muscle onset latencies between 30 - 50 ms; medium latency, functional polysynaptic stretch reflex (M2) with the muscle onset latencies between 50 - 80 ms; triggered reactions with muscle onset latencies between 80 - 120 ms; and voluntary reactions (M3) with muscle onset latency between 120 - 180 ms (Schmidt, 2011; Wilder et al., 1996). Considering the onset latencies of muscle activity, it was previously suggested that abdominal muscle responses to support surface perturbations are likely automatic postural responses triggered as part of a muscle synergy along with other proximal muscles (Carpenter et al., 2008). Stokes et al. (2000) have reported that the trunk muscle responses are likely regulated by monosynaptic reflexes (probably stretch reflex) and medium latency reflexes during trunk loading.

The responses to support surface perturbations observed in our study can likely be classified as medium latency reflexes, as they are too long to be monosynaptic. This means that simple polysynaptic reflexes regulate the trunk neuromuscular system in response to sudden support surface translation perturbations. The polysynaptic reflex responses originate from the muscle spindles and are generally far stronger and more flexible than the monosynaptic reflexes, as well as more involved in movement compensation (Wilder et al., 1996). The polysynaptic reflexes are autogenetic, meaning that they are self-generated, but prior instructions could change the response since the reflex signal travels to the higher centers (i.e., the motor cortex and the cerebellum) during the response (Schmidt 2011).

Average response latencies of the of trunk muscles following support surface translations varied between 70 - 250 ms during sitting and 100 - 200 ms during standing (Preuss and Fung, 2008). Our findings generally agree with this body of literature. However, during direct trunk perturbations applied via a chest harness, reported literature suggested faster trunk muscle responses, ranging between 24 and 68 ms (Cresswell et al., 1994) and 30.7 ms (Granata et al., 2004). These can be can be classified as monosynaptic reflexes. These faster responses may be caused by direct loading of the trunk via a chest harness which can elicit cutaneous afferent reflexes, not present during support surface translations (Carpenter et al., 2008). Hence, the type of perturbation seems to influence the responses latencies of the trunk muscles.

### *4.2. Anticipation of Perturbation*

Average response latencies of the RA-1, RA-2, T9 and L3 muscles were 115.0, 116.6, 103.4 and 117.4 ms, respectively, when the direction and time of perturbation could not be anticipated and decreased to 99.1, 99.8, 90.2 and 96.1 ms, respectively, when both the direction and time of the perturbation could be anticipated. Therefore anticipation of direction and time of perturbation resulted in 16.8 ± 10.0 ms (mean ± SD) average faster trunk muscle responses across all muscles, which is a significant improvement. These results suggest that the anticipation of the direction and time of perturbation decreases trunk muscle response latencies, making them more reflexive. The improved reaction time is indicative of a more efficient response strategy by the central nervous system because it indicates that the system can respond quicker to reduce the load on the spinal disks more effectively which could in turn reduce the risk of injury during balance disturbances (Schmidt 1991; Wilder et al., 1996). Our results also indicate that the time for the trunk to reach the maximum velocity was 8.1 ± 6.3 ms faster during forward perturbations and 6.1 ± 5.5 ms (mean ± SD) faster during backward perturbations when the perturbations could be anticipated. Therefore, earlier activations of trunk muscles lead to the biomechanical advantage of being able to reach the maximum trunk velocity faster, which implies higher acceleration and may be advantageous in stabilizing the trunk more effectively and faster during anticipated perturbations.

Previous studies showed that expectation of a sudden load increased average trunk muscle activations (Aleksiev et al., 1996). During perturbations applied to the head, Kuramochi et al. (2004) reported that neck muscles response amplitudes were greater when the perturbation could be anticipated, but reaction times were not affected. We also hypothesized that trunk muscle activity will increase when perturbations could be anticipated. However, our findings rejected this hypothesis. This is probably because the perturbation and the experimental paradigms were different from our study. However, when the trunk muscles were preloaded before the perturbations, post-perturbation muscle onset latencies were shown to decrease (Shahvarpour et al., 2015). Our results demonstrated that trunk muscle response latencies decreased when the perturbation could be anticipated, despite that the muscles were not preloaded before the perturbation. Since the exact triggering pathways of the trunk muscle reflexes are unknown, it is difficult to speculate why the response latencies were faster with anticipatory information. It was previously suggested that pre-activation of trunk muscles increased the activity of the gamma system, which could have increased the sensitivity of the muscle spindles and the response to their sudden stretching (Stokes et al., 2000). Perhaps an increase in the sensitivity of muscle spindles with anticipatory information triggers the sub-threshold activation of supraspinal neural circuit (i.e., the cerebellum and the motor cortex), which is responsible for decreasing the response latencies of the trunk muscles during sitting perturbations. Overall, the observed influence of the prior information (i.e., anticipation of perturbation) on the trunk muscle reflex responses suggests that the central nervous system can modulate the "readiness" of the trunk using anticipatory information during sitting balance perturbations.

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## Tables

**Table 1:** Analysis of the EMG trunk muscle activity for: rectus abdominis superior to the umbilicus (RA-1) and rectus abdominis inferior to the umbilicus (RA-2) during forward perturbations, and thoracic erector spinae (T9) and lumbar erector spinae (L3) during backward perturbations. Results show the mean ± SD for each muscle of twelve participants. One-way repeated measures analysis of variance (ANOVA) with Tukey post-hoc was used to compare results in four conditions.

| | | | **Condition 1: $D^-T^-$** Direction and time not cued | **Condition 2: $D^-T^+$** Direction not, time cued | **Condition 3: $D^+T^-$** Direction cued, time not | **Condition 4: $D^+T^+$** Direction and time cued | **Catch$^-$** Direction not, time cued; No perturbation | **Catch$^+$** Direction and time cued; No perturbation | **ANOVA** | **Tukey post-hoc** |
|---|---|---|---|---|---|---|---|---|---|---|
| **Tonic muscle activity (µV)** | **Forward** | **RA-1** | 7.1 ± 2.5 | 7.1 ± 2.6 | 7.2 ± 3.0 | 7.1 ± 3.0 | 7.5 ± 3.0 | 6.7 ± 2.9 | | |
| | | **RA-2** | 29.9 ± 4.2 | 30.0 ± 4.2 | 30.1 ± 4.5 | 30.1 ± 4.4 | 30.2 ± 4.6 | 29.3 ± 4.3 | | |
| | **Backward** | **T9** | 7.0 ± 1.9 | 7.1 ± 2.1 | 7.5 ± 2.7 | 7.7 ± 2.6 | 6.9 ± 2.1 | 6.6 ± 2.2 | | |
| | | **L3** | 14.5 ± 3.1 | 14.6 ± 2.9 | 15.2 ± 3.4 | 15.3 ± 3.3 | 14.9 ± 3.0 | 14.2 ± 3.1 | | |
| **Muscle onset time (ms)** | **Forward** | **RA-1** | 115.0 ± 9.7 | 110.4 ± 10.0 | 105.0 ± 8.2 | 99.1 ± 8.3 | | | * | 1-2; 1-3; 1-4; 3-4 |
| | | **RA-2** | 116.6 ± 11.0 | 113.8 ± 11.4 | 109.0 ± 10.0 | 99.8 ± 9.8 | | | * | 1-3; 1-4; 2-4 |
| | **Backward** | **T9** | 103.4 ± 8.5 | 96.1 ± 10.7 | 95.3 ± 12.5 | 90.2 ± 10.8 | | | * | 1-2; 1-3; 1-4; 2-4 |
| | | **L3** | 117.4 ± 13.8 | 108.3 ± 17.6 | 109.6 ± 20.3 | 96.1 ± 17.3 | | | * | 1-2; 1-4; 2-4; 3-4 |
| **Phasic muscle activity (µV)** | **Forward** | **RA-1** | 56.4 ± 43.6 | 61.0 ± 49.8 | 57.5 ± 42.7 | 63.6 ± 56.1 | | | | |
| | | **RA-2** | 47.2 ± 29.2 | 51.3 ± 38.8 | 47.2 ± 25.7 | 49.5 ± 31.1 | | | | |
| | **Backward** | **T9** | 29.0 ± 7.4 | 29.3 ± 6.7 | 29.2 ± 8.0 | 25.7 ± 7.4 | | | | |
| | | **L3** | 19.6 ± 6.3 | 18.8 ± 7.7 | 15.9 ± 5.3 | 16.4 ± 6.3 | | | * | 1-4 |

* $p<0.01$

**Table 2:** Analysis of the center of mass (COM) kinematics during forward and backward perturbations. Results show the mean ± SD of each variable for twelve participants during forward and backward perturbations. One-way analysis of variance (ANOVA) with Tukey post-hoc was used to compare results in four conditions.

| | | **Condition 1:** **$D^-T^-$** Direction and time not cued | **Condition 2:** **$D^-T^+$** Direction not, time cued | **Condition 3:** **$D^+T^-$** Direction cued, time not | **Condition 4:** **$D^+T^+$** Direction and time cued | **ANOVA** | **Tukey post-hoc** |
|---|---|---|---|---|---|---|---|
| **Trunk movement onset (ms)** | **Forward** | 46.3 ± 5.5 | 47.2 ± 4.6 | 46.4 ± 8.6 | 46.8 ± 6.7 | | |
| | **Backward** | 37.8 ± 5.1 | 37.9 ± 5.1 | 38.4 ± 4.9 | 37.5 ± 5.2 | | |
| **Max. trunk displacement (cm)** | **Forward** | 4.9 ± 0.6 | 4.9 ± 0.5 | 4.7 ± 0.5 | 4.7 ± 0.5 | | |
| | **Backward** | 5.1 ± 1.0 | 5.4 ± 0.9 | 5.2 ± 0.8 | 5.0 ± 0.8 | | |
| **Time to max. trunk displacement (ms)** | **Forward** | 327.3 ± 150.0 | 309.4 ± 172.0 | 332.4 ± 210.9 | 328.9 ± 173.7 | | |
| | **Backward** | 372.9 ± 243.8 | 385.4 ± 222.5 | 361.6 ± 186.0 | 358.9 ± 199.2 | | |
| **Max. trunk velocity (cm/s)** | **Forward** | 45.4 ± 4.2 | 44.7 ± 3.4 | 44.2 ± 3.3 | 44.3 ± 3.8 | | |
| | **Backward** | 45.2 ± 2.4 | 46.1 ± 3.0 | 46.1 ± 2.4 | 45.4 ± 3.3 | | |
| **Time to max. trunk velocity (ms)** | **Forward** | 104.1 ± 6.7 | 105.0 ± 5.0 | 94.9 ± 5.6 | 96.0 ± 6.1 | * | 1-3; 1-4; 2-3; 2-4 |
| | **Backward** | 99.3 ± 4.3 | 98.1 ± 5.0 | 95.7 ± 3.1 | 93.2 ± 5.0 | * | 1-3; 1-4; 2-4 |

* $p$<0.01

## Caption to Illustrations

**Figure 1:** Experimental setup showing participant’s posture on the treadmill which was used to apply support surface translation perturbations. Shown are the approximate locations of the upper body segments where the markers were positioned on the subjects’ body to capture the trunk movements. The upper body segments include: i) head (to C7); ii) upper thoracic segment including arms (T1–T6); iii) lower thoracic segment (T7–T12); iv) lumbar trunk segment (L1–L5); and v) pelvis segment. Additional markers were placed on the perturbation platform and the chair to capture the perturbation platform movements.

**Figure 2:** Example of the trunk muscle responses and the chair and center of mass (COM) movements during: a) forward perturbation and b) backward perturbation. Shown is the activity when both direction and time of perturbation could not be anticipated ($D^{-}T^{-}$) and both direction and time of perturbation could be anticipated ($D^{+}T^{+}$) for the rectus abdominis muscle superior to the umbilicus (RA-1), rectus abdominis muscle inferior to the umbilicus (RA-2) in blue, and the thoracic erector spinae muscle (T9) and lumbar erector spinae muscle (L3) in red.

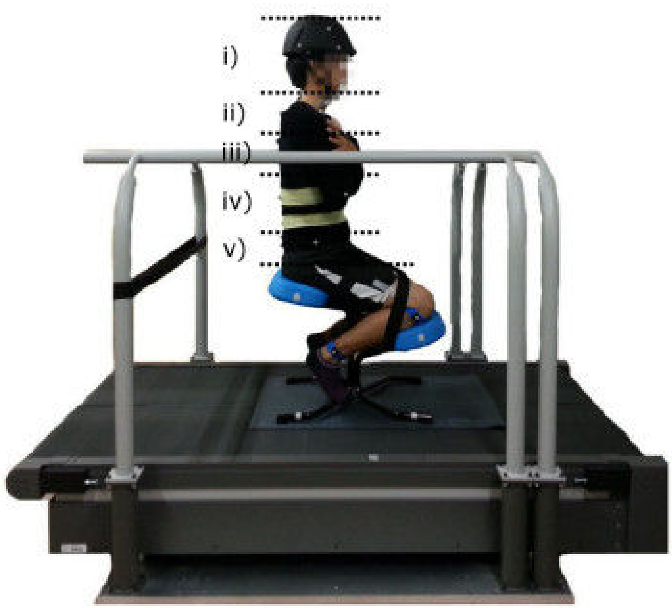


Figure 1

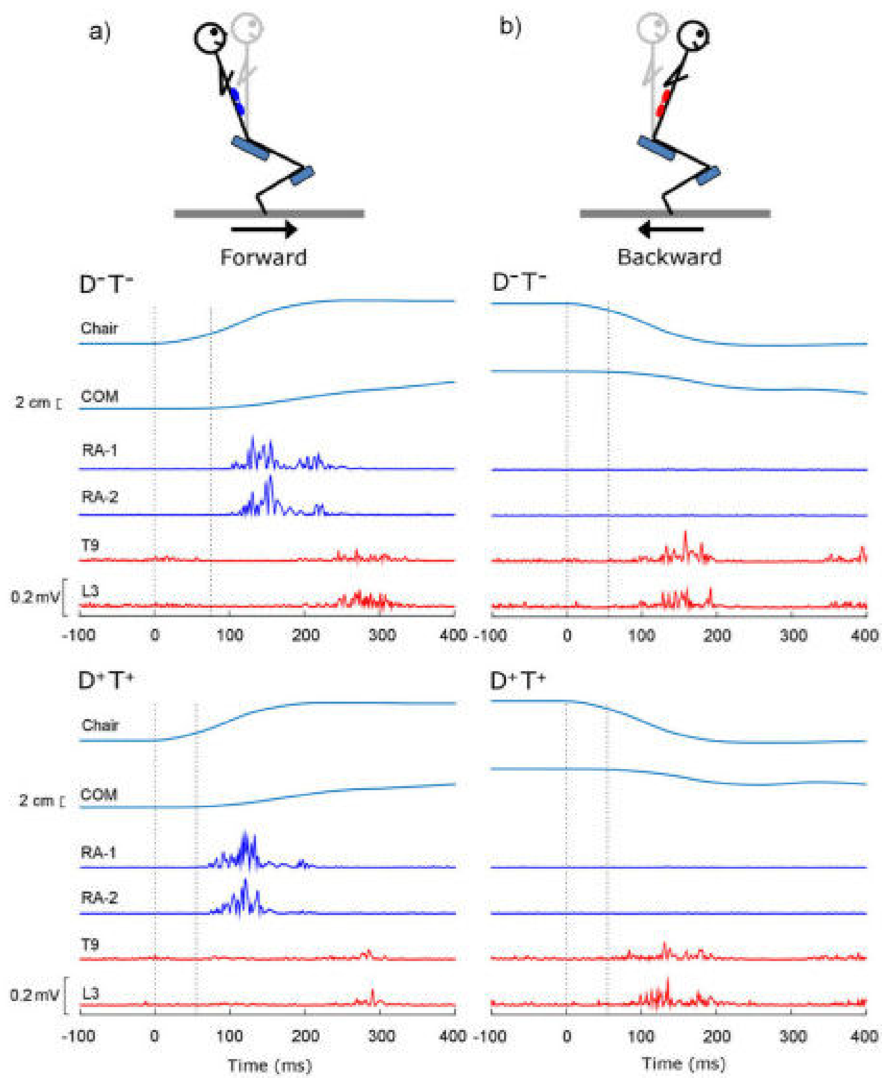
a)
b)
Forward
Backward
D⁻T⁻
D⁻T⁻
Chair
2 cm
COM
RA-1
RA-2
T9
0.2 mV
L3
-100 0 100 200 300 400
-100 0 100 200 300 400
D⁺T⁺
D⁺T⁺
Chair
2 cm
COM
RA-1
RA-2
T9
0.2 mV
L3
-100 0 100 200 300 400
-100 0 100 200 300 400
Time (ms)
Time (ms)

Figure 2