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Effect of predictability of the magnitude of a perturbation on anticipatory and compensatory postural adjustments

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Abstract

Balance maintenance in response to a perturbation could be affected by the predictability of the magnitude of the body disturbance. We investigated anticipatory (APAs) and compensatory (CPAs) postural adjustments in response to perturbations of predictable and unpredictable magnitudes. Twenty young adults received series of perturbations of small or large magnitudes the order of which was varied. Electromyographic activity of six leg and trunk muscles and displacements of the center-of-pressure (COP) were recorded. The muscle onset time, integrals of muscle activity, and COP displacements in the anterior-posterior direction were analyzed during the APA and CPA phases. The results indicated that when the participants were exposed to the repeated perturbation magnitude, so it became predictable, they generated APAs more precisely according to the magnitudes of the perturbation. Moreover, when the magnitude of perturbation changed unpredictably, the participants overestimated or underestimated the magnitudes of the perturbation as they generated APAs based on their prior experience of dealing with the perturbation. The optimal adjustment of APAs occurred after five trials of repeated perturbations. The findings imply that the process of APAs and CPAs generation depends on the accuracy of the predictability of perturbation magnitudes.

Keywords: predictability; perturbation; magnitude; anticipatory postural adjustments; compensatory postural adjustments.

1. Introduction

To maintain a vertical posture, the central nervous system (CNS) employs anticipatory postural adjustments (APAs) and compensatory postural adjustments (CPAs). APAs function as a feed-forward control in regulating the position of the center of mass of the body by activating trunk and leg muscles prior to the predicted upcoming postural perturbation (Massion 1992; Toussaint et al. 1997). CPAs are initiated by the sensory feedback signals and are used to restore the position of the center of mass of the body after perturbation has already occurred (Alexandrov et al. 2005; Le Bozec et al. 2008). Previous studies reported the existence of a relationship between APAs and CPAs: when sufficient APAs were generated prior to the external body perturbation, smaller CPAs were seen after the perturbation which indicated better overall balance control (Santos et al. 2010a; Santos et al. 2010b).

A number of factors can influence the generation of APAs including body stability (Aruin et al. 1998; Aruin and Shiratori 2003), direction (Aruin and Latash 1995) and magnitude (Aruin and Latash 1996) of the perturbation, and predictability of the upcoming perturbations (Burleigh and Horak 1996).

The role of predictability of the magnitude of the perturbation induced in the vertical plane has been studied when catching balls of different weights (Lang and Bastian 1999; Lang and Bastian 2001); it was reported that sitting subjects were able to generate APAs in the upper extremity muscles based on the prediction of the perturbation magnitudes. When the magnitudes of the perturbation were changed unexpectedly, the participants responded to the new magnitude similarly as they responded to the most recent perturbation. Moreover, it took them a couple of trials to generate the optimal anticipatory adjustments in response to the new perturbation magnitudes (Lang and Bastian 1999). It was also reported that adaptation (seen as reduced postural muscle activity and better intersegmental coordination) occurred when a participant's standing balance was challenged by repeated and predictable perturbations (Sozzi et al. 2016). Furthermore, it was described that when participants were required to stand on the moving surface and the perturbation magnitudes and velocities were repeated and became predictable, after five trials, the participants were able to scale the initial postural response in the CPA phase to the parameters of the expected perturbation (Horak and Nashner 1986; Horak et al. 1989). Additionally, the participants seemed to respond to the novel perturbation magnitude based on their experience with the most recent perturbation magnitude. Thus, it was shown that torque responses in the CPA phase were larger when young adults overestimated the actual body perturbation induced by a moving platform and the responses were smaller when the participants underestimated the actual body perturbation (Horak et al. 1989).

It was also reported that humans could adjust the magnitude of APAs if the information about the change in perturbation magnitude was given vocally (Kazennikov and Lipshits 2010; Eckerle et al. 2012; Xie and Wang 2019). Thus, when verbal information about the increase of the perturbation magnitude was available, young adults demonstrated greater APAs. However, when verbal information about the magnitude of the forthcoming perturbation was not available, greater APAs and CPAs were generated to ensure that the task could be completed. For example, when verbal information was not available, APAs were generated based on the largest perturbation magnitude that the subjects experienced during the experiment (Kazennikov and Lipshits 2010; Xie and Wang 2019). Simultaneously, the magnitudes of APAs were consistent across all different perturbation magnitudes (Kazennikov and Lipshits 2010; Xie and Wang 2019). Furthermore, when verbal information about the magnitude of perturbation was unavailable, the APAs were generated at a level similar to the APAs magnitudes elicited for the second largest perturbation magnitude (Eckerle et al. 2012).

While prior research shed light on the role of predictability of the upcoming perturbation in control of posture (Horak et al. 1989; Burleigh and Horak 1996; Aruin et al. 1998; Santos et al. 2010a; Santos et al. 2010b), it is still not clear how the ability to predict the magnitude of a perturbation applied to the shoulders affects the generation of both APAs and CPAs. Thus, the aim of the study was to examine how predictability of magnitude of a perturbation affects the anticipatory and compensatory postural control of vertical stance. Our first hypothesis was that when the magnitude of the forthcoming perturbation changed unpredictably, young adults would generate APAs and CPAs based on their most recent experience of dealing with the perturbation. Our second hypothesis was that when participants were exposed to an expected perturbation the magnitude of which changed, they required less than 10 trials to adjust APAs and CPAs to the new magnitude of the perturbation.

2. Materials and Methods

2.1 Participants

Twenty young adults (10 males and 10 females) without neurological and muscular disorders participated in the experiments. All participants were randomly assigned into two groups (10 participants in each group) based on the sequence of the perturbations: light-heavy-light (LHL) and heavy-light-heavy (HLH). The mean age of the LHL group was 27.60 $\pm$ 1.53 years; mean body mass 63.63 $\pm$ 4.60 kg, and mean height 163.78 $\pm$ 2.36 cm. The mean age of HLH group was 27.50 $\pm$ 1.38 years; mean body mass 68.52 $\pm$ 15.2 kg, and mean height 162.19 $\pm$ 7.2 cm. The gender distribution in each group was 50-50%. There were no statistical differences between groups in all demographic characteristic (p>0.05). All participants signed an informed consent form approved by the Institutional Review Board of the University of Illinois at Chicago before participating in the experiment.

2.2 Procedure

During the experiment, the participants were instructed to stand on the force platform with eyes open, barefoot and with the feet shoulder width apart. The participants stood in front of the pendulum with both their arms, wrists, and fingers extended and they received series of perturbations coming from the front (Santos et al. 2010a). The pendulum was attached to the ceiling and the perturbations were induced in the sagittal plane by an experimenter releasing the pendulum (Fig.1). Different loads, light (L) or heavy (H), (5% and 10% of the participant's body weight respectively) were put in an aluminum bucket (attached to the pendulum's distal end) by an experimenter. The participants were instructed to close their eyes between the series so that they did not know which particular load was placed in the bucket. During the pendulum impact, the participants stood with their eyes open, so they were able to see the upcoming pendulum. Moreover, they were not told which load was placed to the bucket, but they were aware that there were only two different loads (L and H). No advanced warning of the impending perturbation was provided. The perturbations were induced in different sequences: light-heavy-light (LHL) and heavy-light-heavy (HLH) (Fig. 1). The LHL sequence began with 10 trials of the pendulum impact with the light load followed by 15 trials of the heavy load and 10 trials of the light load. The HLH sequence started with 10 trials of the heavy load followed by 15 trials of the light load and 10 trials of the heavy load. Prior to the data collection, participants performed two practice trials of receiving a pendulum impact for each load condition. The time interval between two consecutive trials in all experimental conditions was 10 seconds. The total duration of the experimental session was about 15 minutes.

< Fig. 1 >

The electromyographic (EMG) activity of the right tibialis anterior (TA), medial gastrocnemius (MG), rectus femoris (RF), biceps femoris (BF), rectus abdominis (RA), and erector spinae (ES) muscles was recorded. After the skin was cleaned with alcohol wipes, bipolar disposable surface electrodes (Red Dot, 3 M, USA) were attached over the muscle bellies in pairs with a distance of 25 mm apart. The ground electrode was positioned on the right lateral malleolus. The placements of electrodes were based on recommendations reported in the literature (Basmajian 1980). The EMG signals were collected, filtered, and amplified (10–500 Hz, gain 2000) with an EMG system (Myopac, RUN Technologies, USA).

Ground reaction forces and moments of forces were recorded by the force platform (Model OR-5, AMTI, USA) and the moment of the pendulum impact was recorded by an accelerometer (Model 208CO3, PCB Piezotronics, USA) attached to the pendulum.

The forces, moments of forces, EMGs, and accelerometer signals were synchronized and digitized with a 16-bit resolution at 1000 Hz by means of an analog-to-digital converter and customized LabVIEW 8.6.1 software (National Instruments, USA). The data were stored on a computer for further processing.

2.3 Data processing

All data were processed using the MATLAB software (MathWorks, USA). The signal from the accelerometer was used to determine the timing of the pendulum impact (T_0). All EMG data were filtered with a fourth order high-pass Butterworth filter with a cut-off frequency of 30Hz (Drake and Callaghan 2006). Then the EMG signals were full-wave rectified and linear envelopes were created with a 20Hz low-pass Butterworth filter. The muscle onset (latency) was defined as the first time point within a window of 50ms when the EMG amplitude was greater (activation) or smaller (inhibition) than its baseline value ± 2SD. All the latency detections were checked visually by an experienced researcher for the accuracy. Subsequently, the EMG data in the interval from −100 to +200 ms in relation to T_0 were divided into two epochs and integrated: (1) from −100 to +50 ms (anticipatory postural adjustments, APAs) and (2) from +50 to +200 ms (compensatory postural adjustments, CPAs) (Mohapatra et al. 2012). Baseline activity calculated at the beginning of the trial from -500ms to -450 ms was subtracted from each epoch integrals:

$$\text{EMG\_APAi} = \int_{-100}^{+50} EMGi - 3\int_{-500}^{-450} EMGi$$

$$\text{EMG\_CPAi} = \int_{+50}^{+200} EMGi - 3\int_{-500}^{-450} EMGi$$

where i stands for each of the six muscles.

The center-of-pressure (COP) time series were derived from the force platform data and the COP displacements in the anterior-posterior direction (COP-AP) were used for further analysis. The data were filtered with a fourth order low-pass Butterworth filter with a cut-off frequency of 40Hz (Kanekar and Aruin 2014). Baseline of COP-AP was calculated using the mean value from -500ms to -450ms and the baseline was subtracted from the COP-AP time series. The anticipatory center-of-pressure displacements (COP_{APA}) were calculated as the COP magnitudes at T_0, and compensatory center-of-pressure displacements (COP_{CPA}) were calculated as the maximum displacement after T_0. In addition, the times of the compensatory peak COP displacements (COP_P) in relation to T_0 were calculated.

Experimental data obtained during the perturbation trials were arranged in the following clusters (Fig. 1): the average of last 5 trials before changing the load (L_A and H_B, trials 6-10 and 21-25 respectively), the first trial after the load change ($H1_A$ and $L1_B$, trials 11 and 26 respectively), and the average of last 5 trials after the load change (H_A and L_B, trials 16-20 and 31-35 respectively). Then the data included in the same clusters for both groups were pooled together. For example, the L_A cluster of data for the light-heavy-light sequence and the L_A cluster of data for the heavy-light-heavy sequence (shown in Fig. 1 with the light grey shaded box) were pooled together. Similarly, the H_B cluster of data for the heavy-light-heavy sequence and the H_B cluster of data for the light-heavy-light sequence (shown in Fig. 1 with the dark grey shaded box) were pooled together. The data arranged in the clusters were used to analyze the muscle latencies, EMG integrals and COP displacements for APA and CPA epochs.

2.3.1 Change-point analysis

The change-point analysis was employed to determine the number of trials needed for participants to adjust their postural response after a sudden change of the magnitude of the perturbation. The change-point analysis in variance methods was used previously to identify the location of multiple change points within time series data (Killick et al. 2010; Killick and Eckley 2014). This method can find the most probable changepoint when there are multiple changepoints (Killick et al. 2010). We applied this method to detect the maturing response associated with the adaptation of postural control due to changing the load. The maturing responses are characterized by shifting from a reliance on feedback control for postural adjustments to a feedforward control (Pai and Bhatt 2007). The change-point analysis was performed using data obtained during the LHL and HLH sequences of load changes (Fig. 1). Our preliminary analysis demonstrated that the most prominent change of the APAs integrals was seen in the TA and RF muscles justifying the selection of these two muscles in both LHL and HLH sequences for the change-point analysis. First, a Generalized Addictive Model (GAM) was used to estimate smooth functional relationships of each variable over time. GAM was previously implemented to characterize the effect of potential prognostic factors on disease endpoint (Hastie and Tibshirani 1995). Then, the data were divided into three phases, phase 1 included the data from 1st to 10th trials, phase 2 included the data from 11th to 25th trials, and phase 3 included the data from 26th to 35th trials. Each phase was analyzed with the change-point analysis in variance methods to find the maturing response after load was changed.

2.4 Statistical analysis

Demographic variables (participant's age, weight, height, and gender) were compared between the groups using an independent sample t-test for continuous variables and a chi-square test for categorical data. Skewness and kurtosis were used to assess the normality of the data. All data showed normal distribution. Thus, parametric methods were used for analysis.

A randomized complete block design was used to analyze the differences in muscle latencies, EMG integrals during two epochs for each muscle, COP_{APA}, COP_{CPA} and COP_P between three clusters. All outcome variables were examined using the Generalized Linear Models (GLMs). Pairwise comparison analysis with Fisher's Least Significant Difference (LSD) test was conducted when necessary. The level of significance in all the analyses was set at 0.05. SAS software 9.4 (SAS Institute Inc., Cary NC) was used for all statistical analyses.

3. Results

3.1 EMG traces

The EMG traces obtained from tibialis anterior (TA) and medial gastrocnemius (MG) muscles of a representative participant are shown in Fig. 2. In the APA phase (before T_0), when the magnitude of the perturbation was changed unpredictably, the activation of TA muscle was similar as that in the previous condition. However, when the magnitude of the perturbation was predictable, the activation of TA muscle adjusted according to the magnitude of the perturbations. Thus, comparable activations of TA during the first trial of heavy load ($H1_A$) and the light load (L_A) conditions were observed when the magnitude of perturbation changed from light to heavy. Moreover, when the magnitude of the perturbation was predictable, the activation of TA muscle increased during the heavy load (H_A) compared with that in $H1_A$ and L_A in the light-heavy sequence. EMG traces in the heavy-light sequence behaved similarly as that in the light-heavy sequence.

In the CPA phase (after T_0), the TA and MG became active to reduce the body instability. Thus, in the light-heavy sequence, the TA activity increased in the $H1_A$ condition, compared with that in the L_A and H_A conditions while there is the minimum MG activity in the $H1_A$ condition. Similar trend was seen in the heavy-light sequence. When the magnitudes of the perturbations were predictable, the TA and MG activations adjusted according to the magnitude of the perturbations.

3.2 Muscle latencies

In all the conditions, all the muscles were activated or inhibited before the moment of the perturbation, during the APA phase (Fig. 3). In the light-heavy (LH) sequence, the MG muscle was the first to show an onset among posterior muscles (MG, BF and ES) and the RF muscle was activated earliest among the anterior muscles (RF, TA, and RA). The RF and TA latencies showed significant differences among the conditions (both $p<0.05$). Pairwise comparison analysis with LSD revealed that the RF and TA latencies recorded in the heavy load (H_A) condition were significantly earlier than recorded in the light load (L_A) condition (both $p<0.05$). The order of muscle activation in the heavy-light (HL) sequence was similar as that in the LH sequence. The RF and TA latencies in the HL sequence showed significant differences among the conditions (both $p<0.05$). Pairwise comparison analysis revealed that the RF and TA latencies in the first trial of light load ($L1_B$) condition were earlier than in the light load (L_B) condition (both $p<0.05$). The TA latency in the heavy (H_B) condition was also earlier than in the L_B condition ($p<0.05$).

< Fig. 3 >

3.3 EMG Integrals

The integrals of EMG activities in the APA and CPA phases are shown in Fig. 4. Overall, the APA and CPA integrals of anterior muscles (TA, RF and RA) in unpredictable conditions (the first trial of the heavy load: $H1_A$ and the first trial of the light load: $L1_B$) were similar to that in previous conditions. However, the integrals of anterior muscles changed according to the magnitude of the perturbation when the load became predictable (the light load: L_B and the heavy load: H_A) in both APA and CPA phases.

During the APA phase, there were significant differences among conditions for TA ($p<0.001$), RF ($p<0.001$), BF ($p<0.05$), and RA($p<0.05$) muscles in the light-heavy sequence. Pairwise comparison analysis with LSD demonstrated that the integrals of TA, RF, and RA muscles in H_A condition were significantly larger than that in L_A and $H1_A$ conditions (for TA and RF, all $p<0.001$; for RA, both $p<0.05$). For TA muscle, the integral in $H1_A$ condition was also significantly larger than that in L_A condition ($p<0.001$). Similar changes across conditions could be seen in the integrals of BF muscle: the integral in H_A condition was significantly smaller than that in $H1_A$ and L_A conditions (both $p<0.05$). Additionally, the APA integral of RA muscle in H_A condition was significantly larger than that in L_A and $H1_A$ conditions (both $p<0.05$). In the heavy-light sequence, the APA integrals of TA and RF muscles showed significant differences among conditions (both $p<0.001$). Pairwise comparison analysis confirmed that the integrals of TA and RF muscles were significantly smaller in L_B condition as compared to both $L1_B$ and H_B conditions (for TA, both $p<0.001$; for RF, both $p<0.05$). In both load sequences, anticipatory activation was observed in all the anterior muscles (RA, RF, and TA) and anticipatory inhibition of muscle activities (shown as negative values in Fig. 4) was seen in all posterior muscles (ES, BF, and MG).

During the CPA phase, there were significant differences in the integral magnitudes among conditions for TA ($p<0.001$), RF ($p<0.001$), and RA ($p<0.05$) muscles in the light-heavy sequence. Pairwise comparison analysis with LSD showed that the integrals of TA and RF muscles in L_A condition were significantly smaller than that in H_A and $H1_A$ conditions (all $p<0.001$). For RA muscle, the integral in H_A condition was significantly larger than that in $H1_A$ and L_A conditions (both $p<0.05$). The EMG integrals in the heavy-light sequence were significantly different among conditions for TA ($p<0.001$), RF ($p<0.001$) and ES ($p<0.05$) muscles. Pairwise comparison analysis revealed that the integrals of TA and RF muscles in H_B condition were significantly larger than that in L_B and $L1_B$ conditions (all $p<0.001$). Additionally, the integrals of TA and RF muscles in $L1_B$ condition were significantly larger than that in L_B condition (TA: $p<0.001$; RF, $p<0.05$). For ES muscle, the integral in $L1_B$ condition was significantly larger than that in H_B condition ($p<0.05$). In both sequences, compensatory activation was observed in all the anterior muscles (RA, RF, and TA) in all conditions. However, patterns of muscle activity in posterior muscles were not consistent across conditions.

< Fig. 4 >

3.4 COP displacements

The anticipatory (COP_{APA}) and compensatory (COP_{CPA}) displacements of center-of-pressure are shown in Fig. 5A. Significant differences among conditions were found for the COP_{APA} and COP_{CPA} (all $p<0.001$). Overall, the COP_{APA} in the unpredictable conditions ($H1_A$ and $L1_B$) were similar as that in the previous conditions (L_A and H_B). Consequently, the COP_{CPA} in the unpredictable conditions were modulated as the compensation of the response during APA phase. Pairwise comparison analysis with LSD revealed that the COP_{CPA} in $H1_A$ condition was significantly larger than that in L_A condition in the light-heavy sequence ($p<0.001$). The COP_{CPA} in $L1_B$ condition was significantly smaller than that in H_B condition in the heavy-light sequence ($p<0.001$). Moreover, larger COP_{APA} and COP_{CPA} in H_A condition were exhibited compared with that in L_A condition in the light-heavy sequence (both $p<0.001$) while smaller COP_{APA} and COP_{CPA} in L_B were exhibited compared with that in H_B in the heavy-light sequence (both $p<0.001$). There were also significantly larger COP_{APA} and smaller COP_{CPA} in the H_A condition than that in $H1_A$ condition for the light-heavy sequence (both $p<0.001$). Similarly, significantly smaller COP_{APA} and COP_{CPA} displacements were seen in L_B condition than that in $L1_B$ condition for the heavy-light sequence (both $p<0.001$).

The changes in the time of compensatory peak COP displacements (COP_P) are shown in Fig. 5B. There were significant differences among conditions (both LH and HL sequence p<0.001). Pairwise comparison analysis with LSD revealed that the COP_P in unpredictable conditions were significantly different than in predictable conditions. For light-heavy sequence, the COP_P in $H1_A$ condition was significantly longer than in L_A and H_A conditions (both $p<0.001$). For heavy-light sequence, the COP_P in $L1_B$ condition was significantly shorter than in L_B ($p<0.05$) and H_B ($p<0.001$) conditions.

< Fig. 5>

3.5 Change points to a maturing response

The estimated smooth of the APA integrals of leg muscles (TA and RF) calculated over 35 trials in both the light-heavy-light (LHL) and heavy-light-heavy (HLH) sequences are shown in Fig. 6. Overall, the magnitudes of APA integrals of anterior leg muscles were optimized after 5 trials from the moment when the magnitude of the perturbation was changed. For the LHL sequence, the APA integrals of TA muscle gradually increased from the first change of the load (L to H) in the 11th trial and maintained a plateau after the 16th trials (point a). Similarly, the APA integrals of TA muscle were steadily decreased after the participants experienced the second load change (H to L) in the 26th trial, and maintained a plateau after the 31rd trial (point b). For the HLH sequence, from changing the first load, the APA integrals of TA muscle slowly decreased and maintained a plateau after approximately the 15th trial (point a). For the second load change (H to L), the APA integrals of TA muscle gradually increased and maintained a plateau after approximately the 31rd trial (point b). The estimated smooth of the APA integrals of RF muscle demonstrated a similar trend with that of TA muscle for both sequences. The APA integrals of RF muscle reached the plateau at approximately the 15th trial when the first load was changed. However, no detectable points of adjustment in the APA integrals of RF muscle after the second load change were observed.

< Fig. 6 >

4. Discussion

The study was conducted to investigate the effect of the predictability of the magnitude of a perturbation on anticipatory and compensatory postural adjustments. When the magnitude of the perturbation suddenly changed in both the light-heavy (LH) and heavy-light (HL) sequences, the participants tended to rely on their prior experiences in dealing with the perturbations thus our first hypothesis was supported. Moreover, when participants dealt with the series of perturbations of the changed magnitude, they required about five trials to adjust APAs and CPAs to the new magnitude of the perturbation, thus our second hypothesis was supported.

4.1 Postural control in response to perturbations of expected magnitude

Our results revealed that the amplitudes of the anticipatory activations of muscles were scaled according to the expected perturbation magnitude when the same magnitude of perturbation was repeated. Based on the results of change-point analysis, experiencing a small number of repeated perturbation exposures (5 trials on average) could be enough to restore anticipatory postural adjustments and improve postural stability. In addition, the presence of the plateau state observed when the magnitudes of perturbation were constant (Fig. 6) confirmed that the accurate estimation of the perturbation magnitude resulted in optimal APAs modulation to control posture. These findings are consistent with the outcomes of previous studies (Horak et al. 1989; Lang and Bastian 1999) describing that postural responses were adapted based on the expected perturbation magnitudes. It was also reported previously that a series of perturbations of constant magnitude resulted in action planning which relied on implicit learning acquired from recent experience. Thus, the participants were able to rapidly and implicitly learn to lift an object with appropriate level of grip and load forces for actual weight based on using the somatosensory memory (van Polanen and Davare 2015). This process could be considered as the habituation effect (Keshner et al. 1987; Horak et al. 1989). The results of prior studies and the outcome of the current study taken together suggest that the efficiency of the postural responses appeared to improve when the magnitudes of the perturbation were repeated and became predictable.

The relationship between generating stronger APAs and decreased CPAs (seen as a smaller peak of COP or COM displacement after experiencing the predictable perturbation magnitudes) has been described in the previous literature (Santos et al. 2010a; Santos et al. 2010b; Kanekar and Aruin 2014). It was also reported that the APA magnitude depends on the magnitude of perturbation: larger magnitude of perturbation was associated with larger magnitude of APAs (Aruin and Latash 1996). In agreement with these results, our current study showed that the participants exhibited increased anticipatory activation of anterior muscles in order to adjust to a change of the perturbation magnitudes from light to heavy loads. The generation of larger anticipatory postural adjustments resulted in decrease in the activation of muscles during the CPA phase of postural control. Thus, it looks like the coordinated activation of the anterior leg muscles (RF and TA) resulted in larger shift of the body weight in the direction opposite to the perturbation direction in order to resist the heavy perturbation. When the magnitude of the load changed from heavy to light, decrease of the magnitude of the APA and CPA integrals was also observed.

4.2 Postural control when experiencing unpredictable change of the perturbation magnitude

The results of the current study revealed that when the magnitude of the forthcoming perturbation changed unpredictably, young adults participating in the study adjusted their postural responses by taking into account the most recent experience in dealing with the perturbation. This result is in line with the previous literature reporting that changes in anticipatory activation of muscles were programmed in advance based on previous experience (Horak et al. 1989; Forghani et al. 2017). It was also reported that the study participants were not able to accurately estimate the magnitude of the perturbation on their limb in the first trial after the magnitude of perturbation changed unexpectedly. In that event, they initially either overestimated or underestimated the perturbation with an unexpected change of the magnitude and required trial-and-error practice to generate the optimal movement control (Lang and Bastian 1999).

Overestimation happened when our participants had initially received a perturbation of a large magnitude followed by a sudden change to a perturbation of a small magnitude. As a result, the participants generated similar magnitudes of the anticipatory COP displacement (COP_{APA}) in $L1_B$ and the previous conditions (H_B) in the heavy-light sequence: this resulted in significantly smaller compensatory COP displacement (COP_{CPA}) during the CPA phase. Moreover, smaller COP_{CPA} might be correlated with shorter time spending for postural corrections in the CPA phase. This result is consistent with the outcome of a previous study describing that overestimation of the object weight shortened the lifting phase when lifting a small object using one hand (Rens and Davare 2019).

At the same time, underestimation occurred when small magnitudes of perturbations were followed by unexpectedly switching to a large magnitude of perturbation. The results of the current study showed that in the light-heavy sequence the COP_{APA} in $H1_A$ was similar when compared to the previous condition (L_A). However, the COP_{CPA} in $H1_A$ was significantly larger compared to that in L_A condition due to unexpected occurrence of a larger perturbation leading to postural instability. Additionally, larger COP_{CPA} displacements might be associated with longer time spending on postural corrections in the CPA phase. This result is in line with the previous study (Rens and Davare 2019) describing that underestimation of object weight elongated the lifting phase when lifting a small object using one hand. Increased CPA integrals due to the unexpected change of perturbation magnitudes were related to underestimating the perturbation magnitudes, which could lead to increased mechanical load on postural muscles, postural instability and increased risks for injuries (Xie and Wang 2019).

4.3 Role of practice in optimizing postural control

It was reported that healthy adults and individuals with balance impairment are able to enhance APAs generations after repetitive exposure to perturbations of the same magnitude. Thus, 120 repetitions of throwing a medicine ball allowed to enhance APAs and CPAs in standing participants (Aruin et al. 2015; Aruin et al. 2017; Curuk et al. 2020; Lee et al. 2020). The outcomes of these prior studies, however, did not provide information if a smaller number of repeated exposures to perturbations could enhance the APA generation.

The participants in the current study received the series of the perturbations with unpredictable load changes. We observed that in the first trial of the load change, especially when the load magnitude changed from light to heavy, the participants generated less efficient

APAs which is exemplified by delayed latencies and smaller APA integrals of anterior muscles (Fig. 3-4). However, after the participants were repetitively exposed to the same magnitudes of predictable perturbations, their CNS gradually modified muscle responses and COP displacements so the participants were able to generate optimal APAs after 5 trials following the load change (Fig. 6). Our findings are in line with the outcomes of previous studies reporting that when the magnitudes and velocities of the perturbations became predictable, the participants were able to scale the CPAs generations to the expected perturbation after five trials (Horak and Nashner 1986; Horak et al. 1989). Moreover, since we observed rapid improvement in APAs and CPAs modulations during early practices (the first five trials of repetitive exposure) and a plateau after additional practices, it is tempting to suggest that the training-related enhancement of anticipatory and compensatory postural control could be described using the logarithmic law of practice (Schmidt and Lee 2005). Thus, the results of the current study taken together with the outcomes of prior studies might shed light on the amount of practices needed to modulate APAs and CPAs when the perturbation magnitudes change.

Previous studies demonstrated that in case of random exposures to perturbations of different magnitudes the APAs generation was based on the perturbation of the largest magnitude to ensure that the task could be completed (Kazennikov and Lipshits 2010; Xie and Wang 2019). In contrast, in our study repetitive exposures of the perturbations were provided as a blocked practice which resulted in the enhanced generation of the APAs and CPAs according to the magnitudes of the perturbations.

There are some limitations of the study that we would like to mention. First, only young healthy adults participated in the experiments and the sample was relatively small. Second, only two different magnitudes of perturbation (L and H) were used. Third, the effects of only two different sequences in magnitudes of perturbation (LH and HL) were investigated. Future studies are needed to examine the effect of the predictability of perturbation magnitudes on postural control in older adults and individuals with balance deficits.

5. Conclusions

The accurate predictability of the perturbation magnitudes affects the generation of anticipatory and compensatory postural adjustments. When the magnitude of perturbation changes, at least five trials are needed to adjust APAs allowing to optimize the magnitude of CPAs used to restore balance.

Figure Legends

Fig.1 A schematic representation of the experimental setup. The pendulum impact paradigm was used to induce postural perturbations to the participants. There were two sequences of the load change: (A) Light-Heavy-Light (LHL) and (B) Heavy-Light-Heavy (HLH).

Abbreviations. L_A: light load condition in LH sequence; $H1_A$: the first trial of heavy load condition in LH sequence; H_A: heavy load condition in LH sequence; H_B: heavy load condition in HL sequence; $L1_B$: the first trial of light load condition in HL sequence; L_B: light load condition in HL sequence.

Fig.2 EMG traces of the tibialis anterior (TA) and medial gastrocnemius (MG) muscles of a representative participant. The vertical dotted line shows the moment of perturbation impact (T_0). The thin line represents EMG traces of TA and the thick line represents EMG traces of MG. Time scales are in seconds and EMG scales are in arbitrary units. The order of load change was different: (A) Light-Heavy (LH) sequence, (B) Heavy-Light (HL) sequence.

Abbreviations. L_A: light load condition in LH sequence; $H1_A$: the first trial of heavy load condition in LH sequence; H_A: heavy load condition in LH sequence; H_B: heavy load condition in HL sequence; $L1_B$: the first trial of light load condition in HL sequence; L_B: light load condition in HL sequence.

Fig3 Muscle latencies recorded in the (A) Light-Heavy (LH) and (B) Heavy-Light (HL) sequences.

Abbreviations: ES- erector spinae, RA- rectus abdominis, BF- biceps femoris, RF- rectus femoris, MG- medial gastrocnemius, and TA- tibialis anterior. L_A: light load condition in LH sequence; $H1_A$: the first trial of heavy load condition in LH sequence; H_A: heavy load condition in LH sequence; H_B: heavy load condition in HL sequence; $L1_B$: the first trial of light load condition in HL sequence; L_B: light load condition in HL sequence.

Mean (SE) are shown. Time is in milliseconds. Significant differences between conditions are shown with * ($p<0.05$)

Fig.4 EMG integrals of postural muscles during the anticipatory (APA) and compensatory (CPA) phases of postural control. (A) Light-Heavy (LH) sequence. (B) Heavy-Light (HL) sequence.

Abbreviations: ES- erector spinae, RA- rectus abdominis, BF- biceps femoris, RF- rectus femoris, MG- medial gastrocnemius, and TA- tibialis anterior. L_A: light load condition in LH sequence; $H1_A$: the first trial of heavy load condition in LH sequence; H_A: heavy load condition in LH sequence; H_B: heavy load condition in HL sequence; $L1_B$: the first trial of light load condition in HL sequence; L_B: light load condition in HL sequence.

Positive values indicate muscle activation and negative values indicate muscle inhibition relative to background activities. Mean (SE) are shown. Significant differences between conditions are shown with * ($p<0.05$) for APAs and # ($p<0.05$) for CPAs.

Fig.5 Center-of-pressure (COP) data. (A) Anticipatory (COP_{APA}) and Compensatory (COP_{CPA}) COP displacements and (B) Time of compensatory peak COP displacement (COP_P) in the Light-Heavy (LH) and Heavy-Light (HL) sequences. The COP displacements are in meters, and positive values represent displacements in the posterior direction. Time of compensatory peak COP displacement are in milliseconds.

Abbreviations. L_A: light load condition in LH sequence; $H1_A$: the first trial of heavy load condition in LH sequence; H_A: heavy load condition in LH sequence; H_B: heavy load condition in HL sequence; $L1_B$: the first trial of light load condition in HL sequence; L_B: light load condition in HL sequence. Mean (SE) are shown.

Significant differences of COP displacement between conditions are shown with * ($p<0.05$) for COP_{APA} and # ($p<0.05$) for COP_{CPA}. Significant differences of COP_P between conditions are shown with * ($p<0.05$).

Fig.6 A Generalized Additive Model (GAM) fitted to the data of the APA integrals of tibialis anterior (TA) and rectus femoris (RF) muscles. The plots illustrate the estimated smooth of the EMG integrals over 35 trials in the (A) Light-Heavy-Light (LHL) and (B) Heavy-Light-Heavy (HLH) sequences shown as the solid curves. The shaded regions represent the standard errors of the estimated smooth curves. The change points are identified with the dashed arrow lines. a: the change point of the first load change happened at approximately the 15^{th} and 16^{th} trials; b: the change point of the second load change happened at approximately the 31^{st} trial.

Figure1

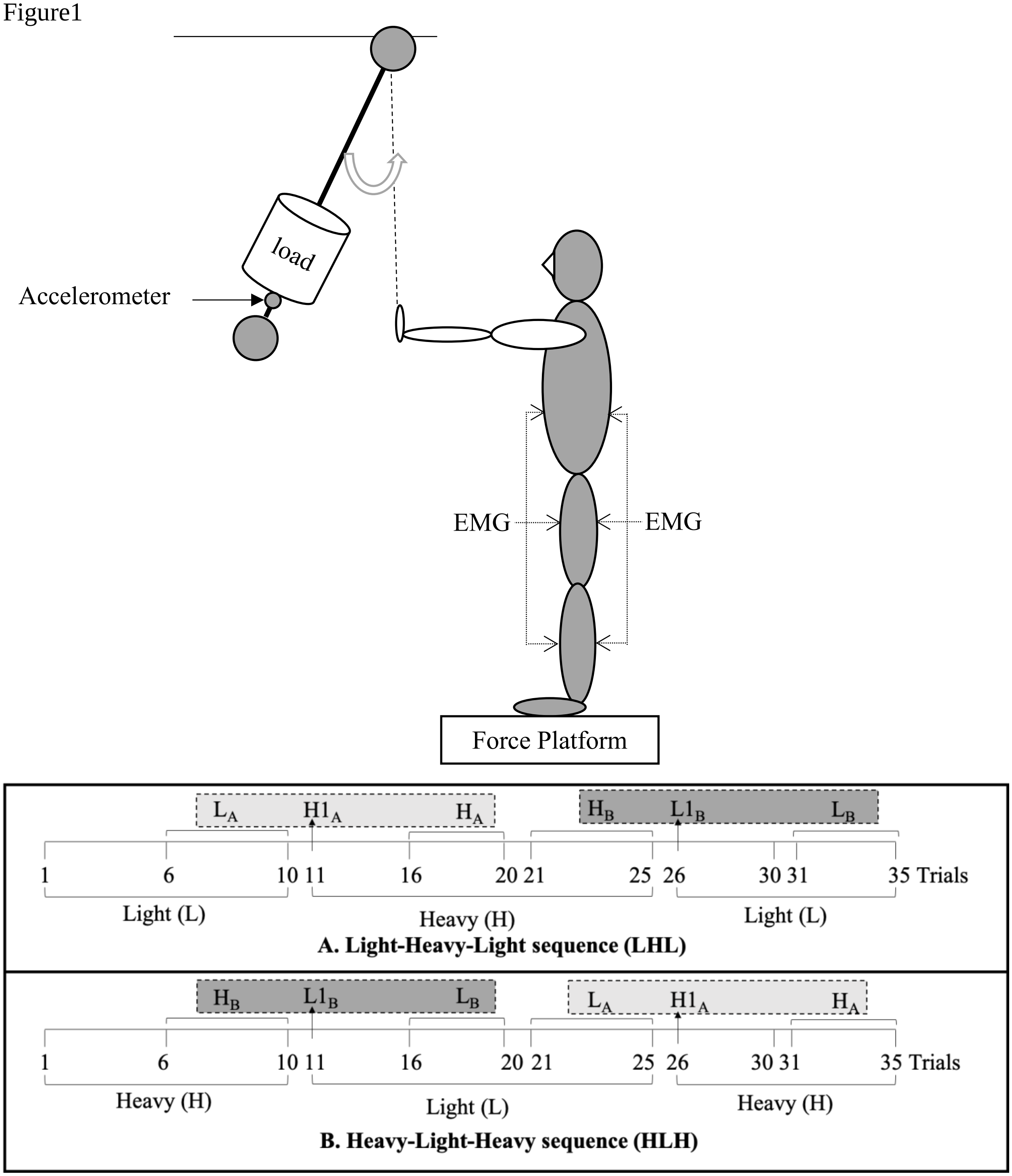
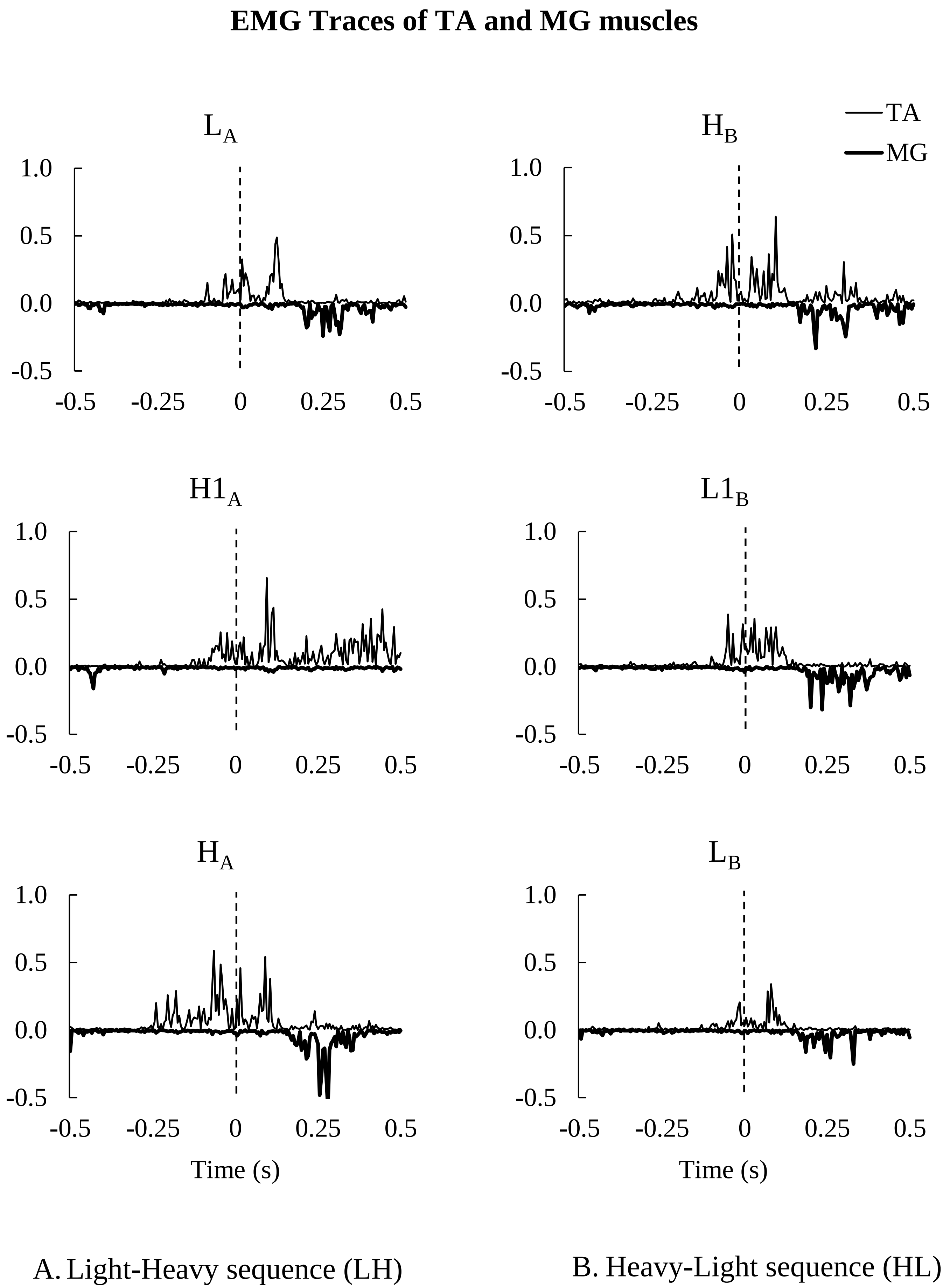
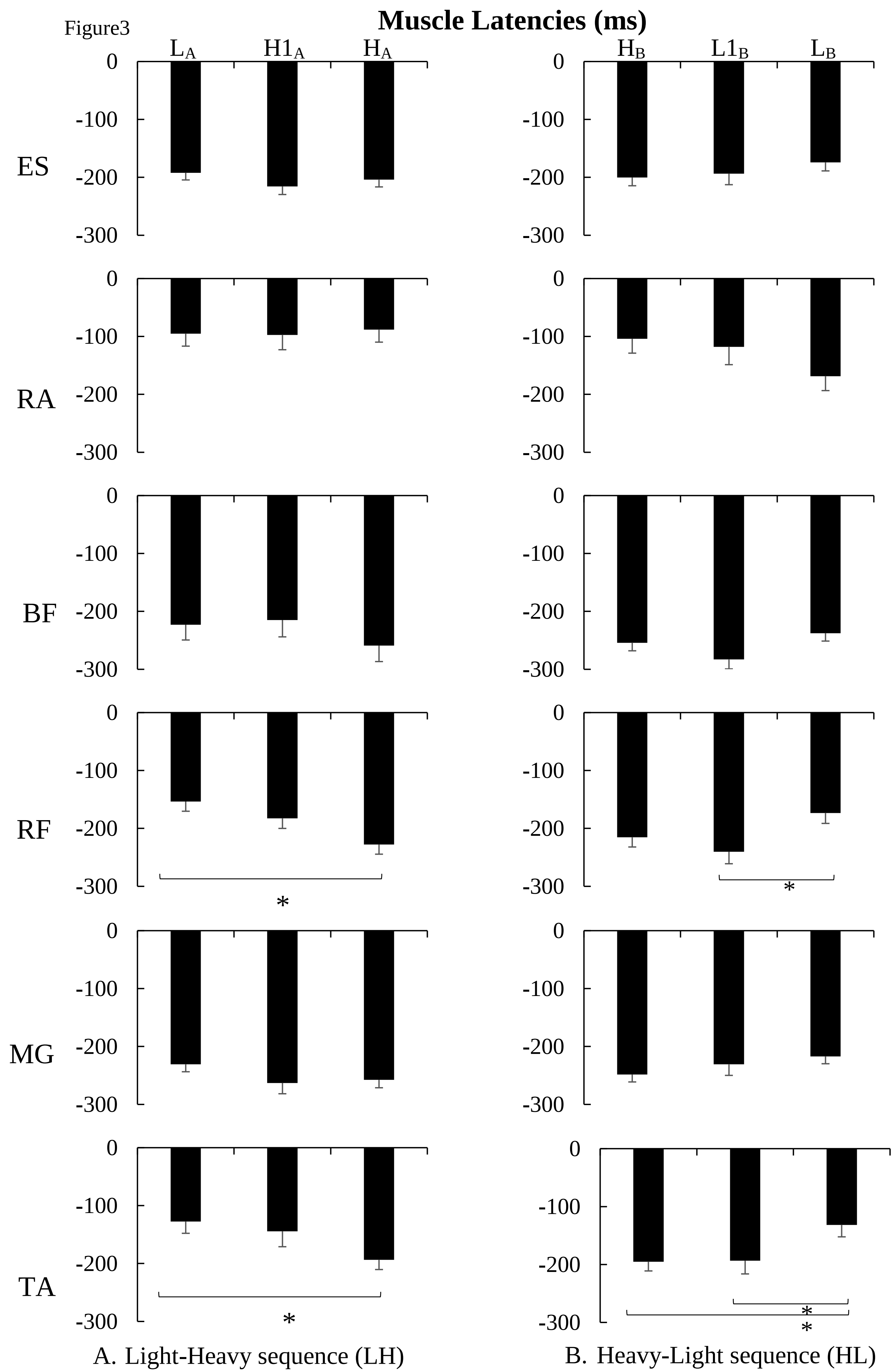

load
Accelerometer
EMG
EMG
Force Platform
L_A $H1_A$ H_A
H_B $L1_B$ L_B
1 6 10 11 16 20 21 25 26 30 31 35 Trials
Light (L)
Heavy (H)
Light (L)
A. Light-Heavy-Light sequence (LHL)
H_B $L1_B$ L_B
L_A $H1_A$ H_A
1 6 10 11 16 20 21 25 26 30 31 35 Trials
Heavy (H)
Light (L)
Heavy (H)
B. Heavy-Light-Heavy sequence (HLH)

Figure2



EMG Traces of TA and MG muscles
TA
MG
L_A
H_B
$H1_A$
$L1_B$
H_A
L_B
1.0
0.5
0.0
-0.5
-0.5
-0.25
0
0.25
0.5
Time (s)
Time (s)
A. Light-Heavy sequence (LH)
B. Heavy-Light sequence (HL)

Figure3



Muscle Latencies (ms)
L_A
H1_A
H_A
H_B
L1_B
L_B
ES
RA
BF
RF
MG
TA
0
-100
-200
-300
*
*
*
*
*
A. Light-Heavy sequence (LH)
B. Heavy-Light sequence (HL)

Figure 4

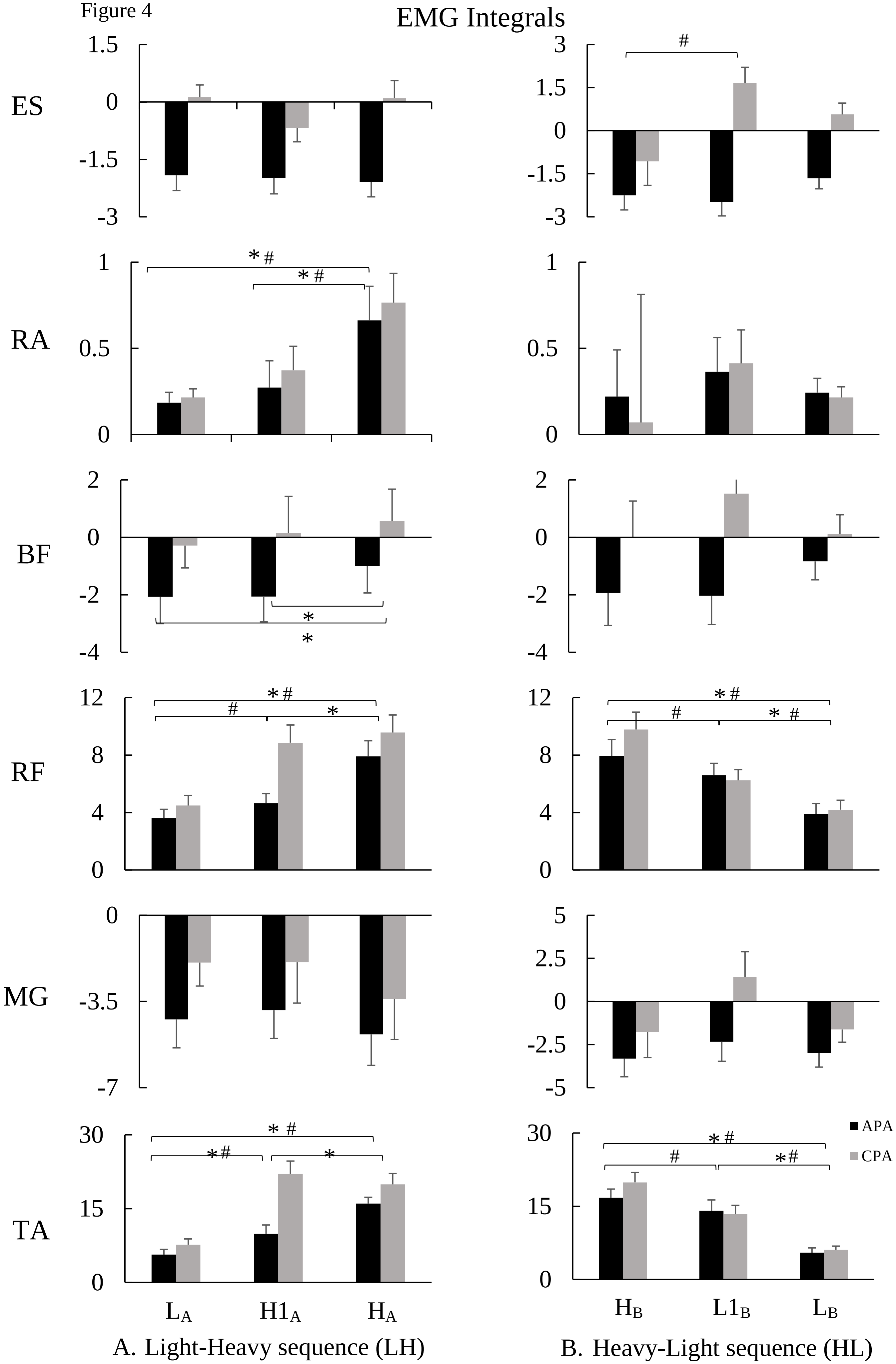
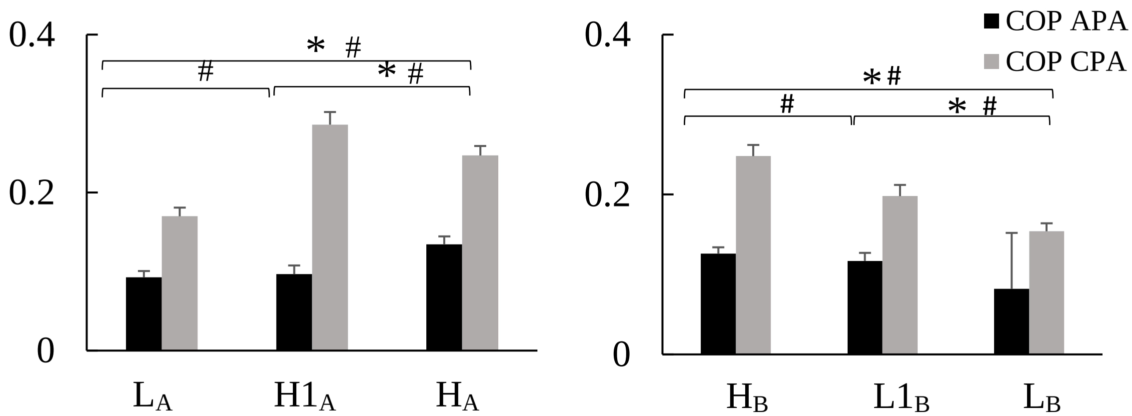

EMG Integrals
ES
RA
BF
RF
MG
TA
APA
CPA
1.5
0
-1.5
-3
3
1.5
0
-1.5
-3
#
1
0.5
0
* #
* #
2
0
-2
-4
*
*
12
8
4
0
* #
#
*
* #
#
* #
0
-3.5
-7
5
2.5
0
-2.5
-5
30
15
0
* #
*#
*
* #
#
*#
L_A
$H1_A$
H_A
H_B
$L1_B$
L_B
A. Light-Heavy sequence (LH)
B. Heavy-Light sequence (HL)

Figure5

Center of Pressure

A. COP displacement (m)



B. Time of compensatory peak COP displacement (ms)

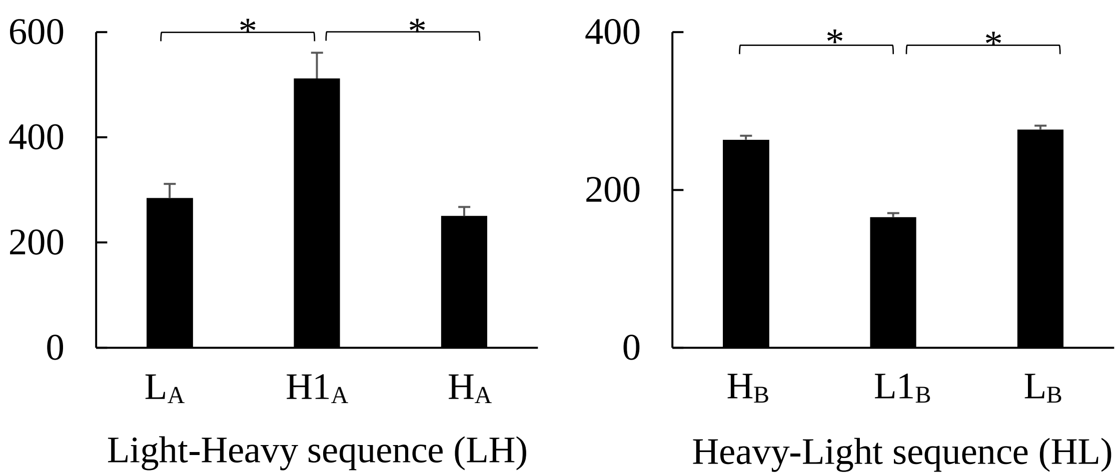
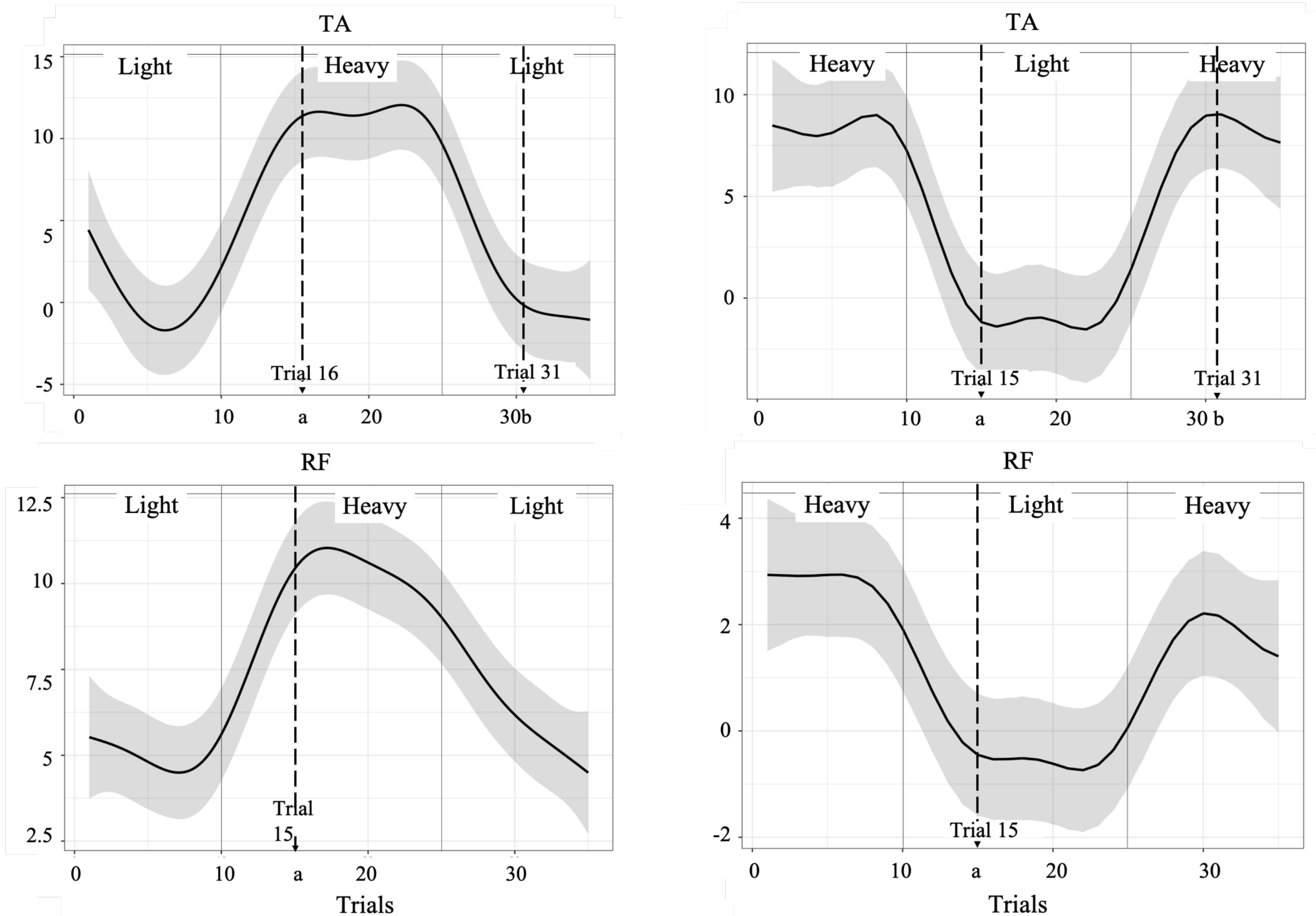


Figure 6

Changes in APA integrals with repeated perturbations



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