Anticipatory response to external repeated perturbations varies with the time interval

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Abstract

Background: The internal model in the brain continues to be refined in response to repeated perturbations against postural stability. We investigate postural responses by anticipatory control that could vary with the interval of perturbations, probably leading to different contributions of learning mechanisms. **Methods**: A total of 12 male volunteers with no neurological deficits (age: 33.33±3.12 S.D.) experienced two sequences of perturbations. Two sequences of perturbations were designed and administered in turn: the first sequence consisted of 24-time repeated perturbations with an interval of 5 seconds, while the second sequence consisted of ones with an interval of 2.5 seconds. A perturbation of a smaller magnitude was inserted into each sequence as a catch trial. Perturbations were given by a force plate moving in the anterior-posterior direction. **Results**: The magnitude of the excursions of the center of pressure (COP) and ankle angle in response to perturbations with a longer interval is greater in comparison to that with a shorter interval ($P < 0.05$). A difference in responses to the perturbation following the catch trial appears in COP ($P < 0.05$), not in ankle angle ($P > 0.05$). These results suggest that while contraction of agonist muscles and co-contraction of antagonistic muscle pairs across the ankle joint for stability operate independently of each other, the refinement of the internal model for a newly trained response can be modulated with stimulus intervals. **Significance**: The dependency of postural responses on the interval could imply that the strength of the learning effect varies with stimulus intervals.

Keywords: External perturbation; postural control; internal model; center of pressure; anticipatory control

INTRODUCTION

The central nervous system (CNS) enables us to adapt ourselves to a series of external stimuli and reach homeostasis. The central control device in the CNS is continuously reprogrammed and refined towards the way that motor outputs become optimal in response to external stimuli (Kim et al. 2014; Kim and Hwang 2018; Laessoe and Voigt 2008; Mohapatra, Krishnan, and Aruin 2012; Redfern et al. 2002). We observed that while the body response has large variability in response to inexperienced stimuli, it shows smaller variability in response as adaptation continues, suggesting that the CNS works to find an optimal solution to regain stability from the stimuli.

While it is the undeniable fact that our body goes through a learning process for adaptation to motor activity, the learning rate and learning strength can vary with time intervals of training. Indeed there is plenty of evidence that different frequencies of training lead to involvements of different types of learning or learning in different neural substrates. Several studies showed that there exist the optimal intervals that lead to the best consolidation and retention (Criscimagna-Hemminger and Shadmehr 2008; Krakauer, Ghez, and Ghilardi 2005; Pekny and Shadmehr 2015; Yamada, Itaguchi, and Fukuzawa 2019). A certain time interval enhances the effect of motor learning, prolonging motor memory. While some argued that enough time intervals between trainings is necessary to consolidate motor memory (Criscimagna-Hemminger and Shadmehr 2008; Pekny and Shadmehr 2015), some asserted that long time intervals can result in time decay of motor memory (Nettersheim et al. 2015; Tanaka, Krakauer, and Sejnowski 2012). It might be beneficial to determine the optimal time interval according to the type of the task to be trained in order to maximize the effect of motor training.

Responding to external stimuli and refining the internal models also depend on the intervals of the stimuli. Taking finger sequence responding tasks for example, studies revealed that a longer interval between stimuli leads to a greater learning effect (Miyawaki 2006; Willingham and Goedert-Eschmann 1999). Longer intervals allow participants for time to accumulate explicit knowledge on the sequence and encode it into the CNS responding to the stimuli. The accumulated explicit knowledge in addition to implicit learning that lacks awareness results in faster responses and enhanced learning effects in tasks where the anticipatory factor is pronounced. Either the so-called implicit learning or explicit learning can be involved predominantly according to the frequency of stimuli, facilitating different neural substrates for learning (Eichenbaum 1999; Grahn, Parkinson, and Owen 2009; Reber and Squire 1994; Yang and Li 2012). Again we could humbly speculate that different time lapses of motor activity lead to involvements of different types of learning or learning in different neural substrates or learning mechanisms.

It remains as a fully unexplored question whether the frequency of stimuli to postural stability affects the learning rate and learning strength. It could be hypothesized that automatic postural responses that are typically made from the association between online feedback and feedforward control are influenced by intervals of repeated perturbations. While online feedback enables the CNS to perceive the environment in real time, muscle activation is centrally modulated through an anticipatory manner to recover postural stability as trials advance, which is a product of learning (Franklin, Wolpert, and Franklin 2012; Kim and Hwang 2018; Wolpert and Miall 1996). Typically, continuous movement tasks are assumed to rely more on implicit learning, in comparison to discrete tasks including finger sequence responding, due to relative difficulty of recognizing and encoding errors into the control system (Franklin, Wolpert, and Franklin 2012; Wolpert and Miall 1996; Yamada, Itaguchi, and Fukuzawa 2019). Allowance of time for participants to be consciously reminded of a continuous response in a repeated task would bring about involvements of different neural learning regions. Accordingly, the degree of the learning effect would be distinguished. Yet no attempt to address this curiosity has been made, although the answer would be helpful in creating effective clinical strategies, like in perturbation training that aims at reducing falling.

In this study, we had participants with no neurological disorder experience two types of a series of anterior-posterior translational perturbations. The two types were differentiated by the interval of perturbations. We investigated if/how intervals of perturbations modulate motor responses and learning strength in terms of the center of pressure and ankle excursion.

METHODS

Participants

A total of 12 male volunteers, from Kyungpook National University, ranging in age from 25 to 37 years (age: 33.33±3.12 standard deviations (SD); height: 172.92±4.44 cm; weight: 71.25±8.08 kg), were recruited for this study. All participants reported no histories of neurological or motor deficits. None of the participants had previous experience with perturbation experiments and were not made aware of our experimental design. All participants gave written informed consent to participant in the study. The experiment was approved by Kyungpook National University's Institutional Review Board.

Apparatus

Fig. 1 displays a schematic of the experimental setup and experimental data from this setup. The experimental setup was composed of a platform on which participants stood, two miniature motion tracking devices, and a personal computer (PC) running Windows 10 (Microsoft Corp. Redmond, WA, USA). The platform was built with a force plate (EzForce Plate, i2A systems Co., Ltd., Daejeon, Korea) to be used for measuring COP on a linear guide rail (8 mm/revolution) that converted a brushed DC motor's (RE65, Maxon Motor, Sachseln, Switzerland) rotary motion into anterior-posterior translational motion. We designed two kinds of perturbations that caused body sway in the sagittal plane: small and large perturbations. While the small perturbation was designed to produce a displacement of 2 cm for 0.3 s, the large perturbation generated a displacement of 6 cm for 0.3 s. The force plate was designed to immediately move back to the original position for 0.3 s. The design of these perturbations was believed to elicit a muscular and biomechanical response to the perturbations.

The two motion tracking units (MPU9250, InvenSense Inc., San Jose, USA) measured the acceleration values of the lower and upper body, respectively, in the anterior-posterior, a_{AP}, craniocaudal (a_{CC}) and lateral (a_L) directions. 3D printed cases were devised to include each of the tracking units to allow firm placement of these units on the participant's body aligned in the three directions. One unit was attached at 5% of the total height below the knee joint while the other unit was attached at 13% of the total height above the hip joint. Acceleration values were used to calculate the angles of the lower and upper body with regard to the vertical line, respectively, using the following equation (Kim and Hwang 2018):

$$\theta = tan^{-1}\left(\frac{a_{AP}}{\sqrt{a_{AP}^2 + a_L^2}}\right)$$

Data including the DC motor angle, COP and body acceleration were acquired using a PC, and a control command was sent to the motor using a signal processing board (Batuino, i2A systems Co., Ltd., Daejeon, Korea), with a sampling frequency of 500 Hz. No filters were applied to the kinematic data to minimize signal distortion.
White noise was presented through headphones to eliminate the effect of noise from the apparatus on postural control.

Procedure

Throughout the experiment, participants stood barefoot on the force plate with their feet apart in a comfortable stance and their arms crossed over the chest. The participants were instructed to recover their balance every time a perturbation was administered and to avoid taking a step so long as they could avoid falling. They were also recommended to use the ankle strategy as far as possible, instead of the hip strategy or other strategies. The participants were not informed of the objective or design of the experiment.

The experiment consisted of a practice phase and a main phase. Before the main phase began, the practice phase was introduced to allow participants to familiarize themselves with the large and small perturbations. Participants were presented each perturbation twice.

In the main phase, all participants were evenly and randomly divided into two groups. Two sequences of perturbations were designed and administered in turn. Each group began with one of the two sequences. In Sequence 1, the large perturbation was repeated 19 times, followed by one small perturbation, 2 large perturbations, and 2 small perturbations. The perturbation interval between perturbations was set as 5 seconds. In Sequence 2, the same sequence of the perturbations as Sequence 1 was designed but the perturbation interval between perturbations was set as 2.5 seconds. We confirmed that participants were expected to regain and stabilize their original posture before the onset of the next perturbation. A break time of 5 minutes was provided between the two sequences in an effort to avoid fatigue and reduce the learning effect from the proceeding sequences.

Signal post-processing and Measures

All data analyses were completed using custom software (MATLAB vR2018b, Mathworks, Natick, MA). The levels of ankle angle and COP were adjusted to 0 at the time when the perturbations began. To extract participants' postural strategies from these data, we considered how large the deviation from their original position was (Excursion I) and in what ranges they moved in response to perturbations (Excursion II).

Excursion I was defined as the distance between the maximum deviation in COP and ankle angle resulting from the perturbation and their original position before the perturbation. The maximum deviation could be regarded as the first effort to regain postural stability. Excursion II denoted the total anterior–posterior movement of COP and the kinematic data in response to the perturbation. Since COP is closely proportional to the ankle moment, Excursions I and II for COP could indicate how much ankle moment was generated to regain postural stability (Kim and Hwang 2018). Also, Excursions I and II for ankle angle would indicate the extent of body sway caused by the perturbations.

To investigate the influence of the response to the adjacent previous trial on that of the current trial, we calculated differences in Excursions I and II of COP and ankle angle between the current trial and adjacent previous trial.

The learning effect of repetition of trials was investigated in two ways: one way was to investigate whether a downward trend across trials (from Trial 1 to Trial 19) was observed and the other was to examine robustness to the catch trial (Trial 20). Trends in differences between trials were also investigated.

Statistical analysis

A repeated-measures analysis of variance (ANOVA), with sequence and trial as the independent variables, was used to the evaluate performance changes across repeated measurements. If the sphericity assumption in ANOVAs was violated, then Greenhouse-Geisser adjusted p-values were used. Bonferroni post-hoc tests were conducted if a significant interaction effect was found. The statistical analyses were performed with SPSS version 20.0 (SPSS Inc., Chicago, USA) and the significance level was set at 0.05. All analyses were preceded by Shapiro–Wilk tests of normality and their results were employed only when normality was not violated.

RESULTS

A. Adaptation to repeated perturbations (Trial 1 to Trial 19)

Repeated-measures ANOVAs were conducted on each measure from Trial 1 to Trial 19 with trial (19 levels: Trials 1–19) and sequence (2 levels: Sequences 1 and 2) as within-subjects variables. Fig. 2 shows the overall trends of Excursion I and Excursion II of COP and ankle angle across trials.

1. COP: ANOVA on Excursion I of COP showed a significant main effect of sequence [$F(1, 11)=5.668$; $p=0.036$; $\eta_p^2=0.340$] and a significant main effect of trial [$F(18, 198)=7.340$; $p<0.001$; $\eta_p^2=0.400$]. The interaction effect was not significant ($p>0.1$). The results would imply that that the sequence with a shorter interval generated a smaller Excursion I than that of a longer interval and that both of the sequences led to the learning effect. ANOVA on Excursion II of COP produced a significant main effect of sequence [$F(1, 11)=9.359$; $p=0.001$; $\eta_p^2=0.460$] and a significant main effect of trial [$F(18, 198)=9.187$; $p<0.001$; $\eta_p^2=0.455$]. The interaction effect was not significant ($p=0.076$). The results would also suggest that that the sequence with a shorter interval generated a smaller Excursion II than that of a longer interval and that both of the sequences led to the learning effect.

2. Ankle angle: ANOVA on Excursion I of ankle angle showed a significant main effect of sequence [$F(1, 11)=19.338$; $p=0.001$; $\eta_p^2=0.637$] and a significant main effect of trial [$F(18, 198)=5.349$; $p<0.001$; $\eta_p^2=0.327$]. The interaction effect was not significant ($p=0.061$). The results would imply that that the sequence with a shorter interval generated a smaller Excursion I in ankle angle than that of a longer interval and that both of the sequences showed adaptation. ANOVA on Excursion II of ankle angle produced a significant main effect of sequence [$F(1, 11)=18.937$; $p=0.001$; $\eta_p^2=0.633$] and a significant main effect of trial [$F(18, 198)=3.272$; $p<0.001$; $\eta_p^2=0.229$]. The interaction effect was not significant ($p>0.1$). The results would imply that that the sequence with a shorter interval led to a smaller Excursion II than that of a longer interval and that both of the sequences led to adaptation.

B. Robust to the catch trial (Trial 20)

Repeated-measures ANOVAs were conducted on each measure over Trials 19, 21 and 22 with trial (3 levels) and sequence (2 levels: Sequences 1 and 2) as within-subjects variables.

1. COP: ANOVA on Excursion I of COP during the three trials showed a significant main effect of sequence [$F(1, 11)=9.508$; $p=0.010$; $\eta_p^2=0.464$]. A pairwise comparison revealed a significant difference between two sequences at Trial 21 ($p=0.026$), as seen in Fig. 3. ANOVA on Excursion II of COP showed a significant main effect of sequence [$F(1, 11)=8.857$; $p=0.013$; $\eta_p^2=0.446$] and a significant main effect of trial [$F(2, 22)=11.302$; $p<0.001$; $\eta_p^2=0.507$]. A pairwise comparison showed significant differences between two sequences at Trials 19 and 21 ($p<0.05$). The results would demonstrate the different effects of the two sequences on responses to the trained perturbation following the catch trial (Trial 20).
2. Ankle angle: ANOVA on Excursion I of ankle angle showed a significant main effect of sequence [$F(1, 11)=40.355$; $p<0.001$; $\eta_p^2=0.786$] and a significant main effect of trial [$F(2, 22)=18.720$; $p<0.001$; $\eta_p^2=0.630$]. The interaction effect was not significant ($p>0.2$). A pairwise comparison showed a significant difference between two sequences at only Trial 19 ($p=0.016$). ANOVA on Excursion II of ankle angle revealed a significant main effect of sequence [$F(1, 11)=16.433$; $p=0.002$; $\eta_p^2=0.599$]. A

pairwise comparison showed significant differences between two sequences at Trials 19, 21 and 22 ($p<0.01$), as displayed in Fig. 3. The results of Excursion II would demonstrate that a shorter interval led to a smaller excursion of ankle angle over the responses to perturbations.

DISCUSSION

This study tested the hypothesis that different time intervals of stimuli to postural stability lead to involvements of different neural substrates or learning mechanisms. We revealed that a train of perturbations with shorter intervals as well as longer intervals provoke adaptation or the learning effect (the main effect of trial: $p<0.05$), but it occurs with no significant different learning rates (interaction $p>0.05$). Interestingly, we found that the degree of consolidation of learning depends on the time interval from the significant differences between the two groups in measures at Trial 21 following a catch trial. In this section, we discuss it with supporting evidence presented by other studies.

The primitive finding of this study might be that a train of perturbations with shorter intervals results in smaller excursions of ankle angle in response. Despite perturbations with the same profile presented to the two groups, participants show different responses in terms of the degree of body sway. These results might come from the hypothetical theory that the human motor system relies on anticipatory control based on priori experiences (Kim and Hwang 2018). We could interpret the results as participants tended to employ greater muscle co-contraction to minimize body sway caused by faster repetitions of perturbations. An increase in co-contraction typically occurs to minimize postural sway (Nelson-Wong et al. 2009; Reynolds 2010). Increasing joint stiffness through muscle co-contraction might partially originate from fear about the fast repetition of perturbations. If we have fear when facing a postural threat, we employ a stiff ankle strategy to assure stability (Okada et al. 2001; Young and Mark Williams 2015).

The results that a shorter time interval leads to a smaller excursion in COP response could also be attributed mainly to the stiff ankle strategy. It is reasonable to speculate that stiffer ankle joint through greater co-contraction between the muscles in the antagonistic setup spanning the ankle joint leads to a smaller body sway, and a smaller body sway results in a smaller excursion in COP. A larger body sway leads to a larger extent of body leaning that requires a larger torque at the ankle to upright the leaned body against gravity. These results are in agreement with those of our previous study (Kim and Hwang 2018). Our results are also in accordance with the empirical results of a study, though they concluded a different opinion about ankle joint stiffness (Ersal, McCrory, and Sienko 2014).

The interesting finding is perhaps about the responses to perturbations in trials following a catch trial (at Trial 20). Those responses would imply the robustness of the learning effect to an unlearned stimulus. The downward COP responses demonstrate motor learning through updating the internal model. Central activation is modulated in anticipation of postural sway (Beretta et al. 2019; Kanekar and Aruin 2014; Kim and Hwang 2018; Mohapatra, Krishnan, and Aruin 2012). We could reasonably regard that the plateau of the learning effect starts at least from Trial 15 for both sequences (with different time intervals). The train of perturbations with a longer time interval exhibits a different response to Trial 21 in comparison to that with a shorter interval ($p<0.05$). While the COP at Trial 21 responses show a significant difference between the two groups, Excursion I for ankle angle does not, suggesting that the difference in ankle stiffness between the two groups is not significant. The possible reason would be that Excursion I for ankle angle reflects the extent of body sway or the extent of muscle co-contraction which is primarily affected by the very previous trial, while Excursion I for COP reflects motor responses trained through repetitions of perturbations (Kim and Hwang 2018). Contraction of agonist muscles and co-contraction of antagonistic muscle pairs across the ankle joint are employed to stabilize posture, the two components are believed to operate independently of each other. Excursion Is for COP and ankle angle are a measure made in a range where online feedback works (Kim 2019; Kistemaker, Van Soest, and Bobbert 2006; Miall et al. 1993). Rather than co-contraction simply achieved through an anticipatory manner from the previous trial, perceiving the perturbation and incorporating it into the motor response (i.e. COP) might reflect the refinement of the internal model that pertains to motor responses. Excursion II for COP could also be evidence of this theory. Though significant differences at Trials 19 and 21, the p-value for Trial 21 is greater than that for Trial 19 (we believe that the significant differences for Trial 19 would not be meaningful). This could straightforwardly imply the different strengths of the learning effects of the two trains that might be linked to the degree of an effort to minimize the influence by the catch trial. That is, a longer interval leads to a stronger learning effect. The group with a longer interval tends to retrieve the response used to the perturbations following the catch trial. Responses at Trial 23 could imply a stronger learning effect of a longer interval.

Then what factor originating from the difference in interval made the difference in response between the two groups? Perhaps the difference is mainly because a longer interval allows for time to program and consolidate the motor system to respond to the perturbation. A longer interval would lead to the involvement of conscious learning that facilitates motor learning (Karabanov and Ullén 2008; Miyawaki 2006). As mentioned in Introduction, finger sequence learning studies found that a longer interval between stimuli leads to an enhanced learning effect (Karabanov and Ullén 2008; Willingham and Goedert-Eschmann 1999). The possibility of the involvement of explicit knowledge in sequence learning would be the main contributor to faster responses and enhanced learning effects in tasks. Indeed explicit knowledge on learning facilitates different neural substrates during motor execution and substantially affects the formation of the anticipatory mechanism. Studies suggest that the frontal cortex and basal ganglia are related to implicit memory while the hippocampus and temporal-parietal cortex are relevant to explicit memory (Eichenbaum 1999; Grahn, Parkinson, and Owen 2009; Reber and Squire 1994; Yang and Li 2012). The studies that showed that prolonged intervals degrade motor learning also evidence that the anticipatory component mainly governed by the internal model can be modulated by intervals. They asserted that too long intervals (amounting to several hours) could allow factors to intervene the formation of the internal model for trained motoric behaviors, leading to a reduction in consolidation. From a series of empirical evidence regarding the influence of time intervals, this study reasonably speculates that time intervals are a critical factor to building up internal models for a novel motor response.

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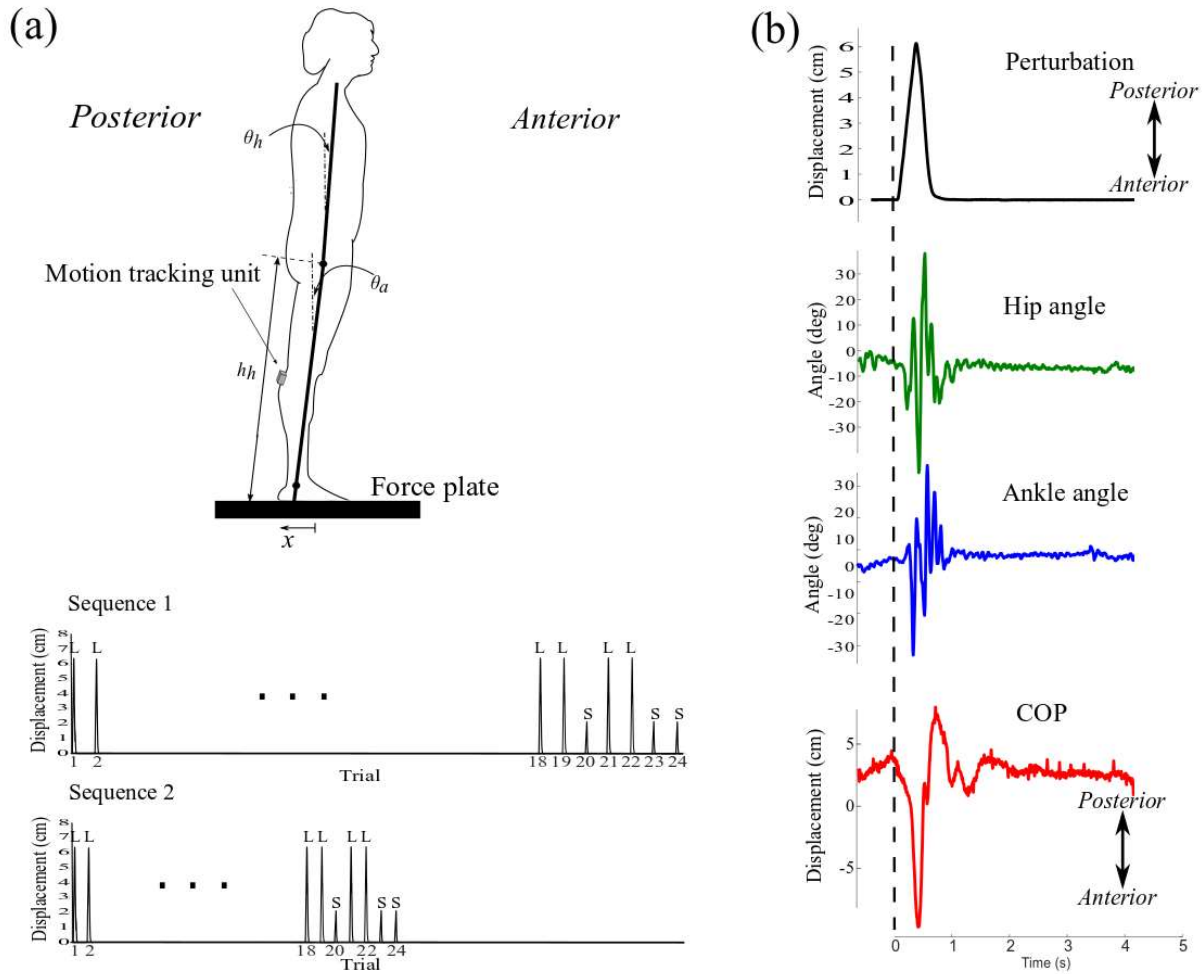

Fig. 1 (a) A schematic of the experimental setup and definitions of the ankle angle q_a, hip angle q_h, and hip height h. Sequence 1 and Sequence 2 consist of 19 large perturbations followed by followed by one small perturbation, 2 large perturbations, and 2 small perturbations. The perturbation interval between perturbations of Sequence 1 is set as 5 seconds, while that of Sequence 2 was set as 2.5 seconds. (b) Experimental data obtained from a participant for Trial 2 in Sequence 1: displacement of the force plate, hip and ankle angles, and COP from the left leg. The dashed line indicates the time at the onset of the perturbation. All data are aligned to the dashed line.

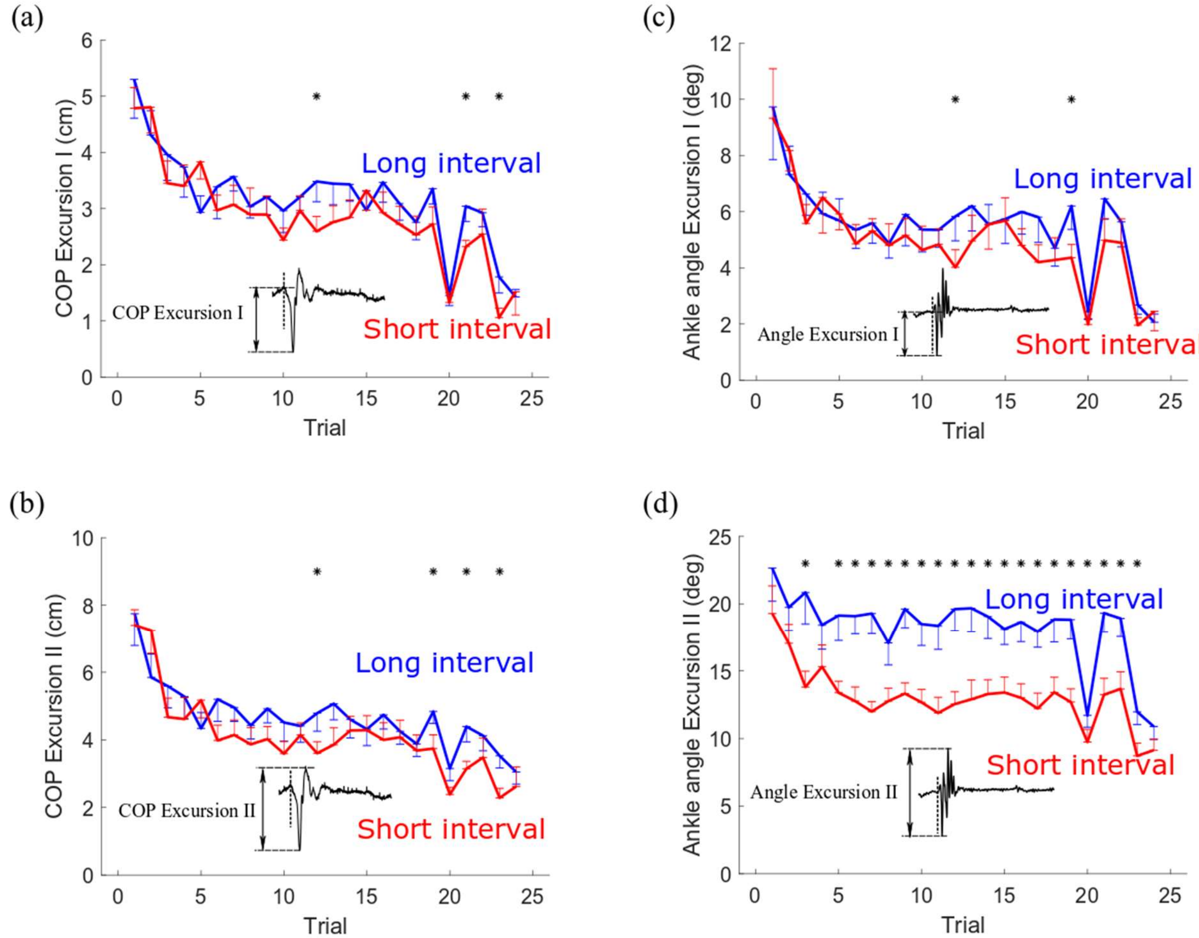

Fig 2. Mean by sequence of the magnitudes of Excursion I and Excursion II of COP and ankle angle for Trial 1 to Trial 24 (Error bars are ± 1 standard deviation of the mean). The inlets display the definitions of Excursion I and Excursion II for COP and ankle angle.

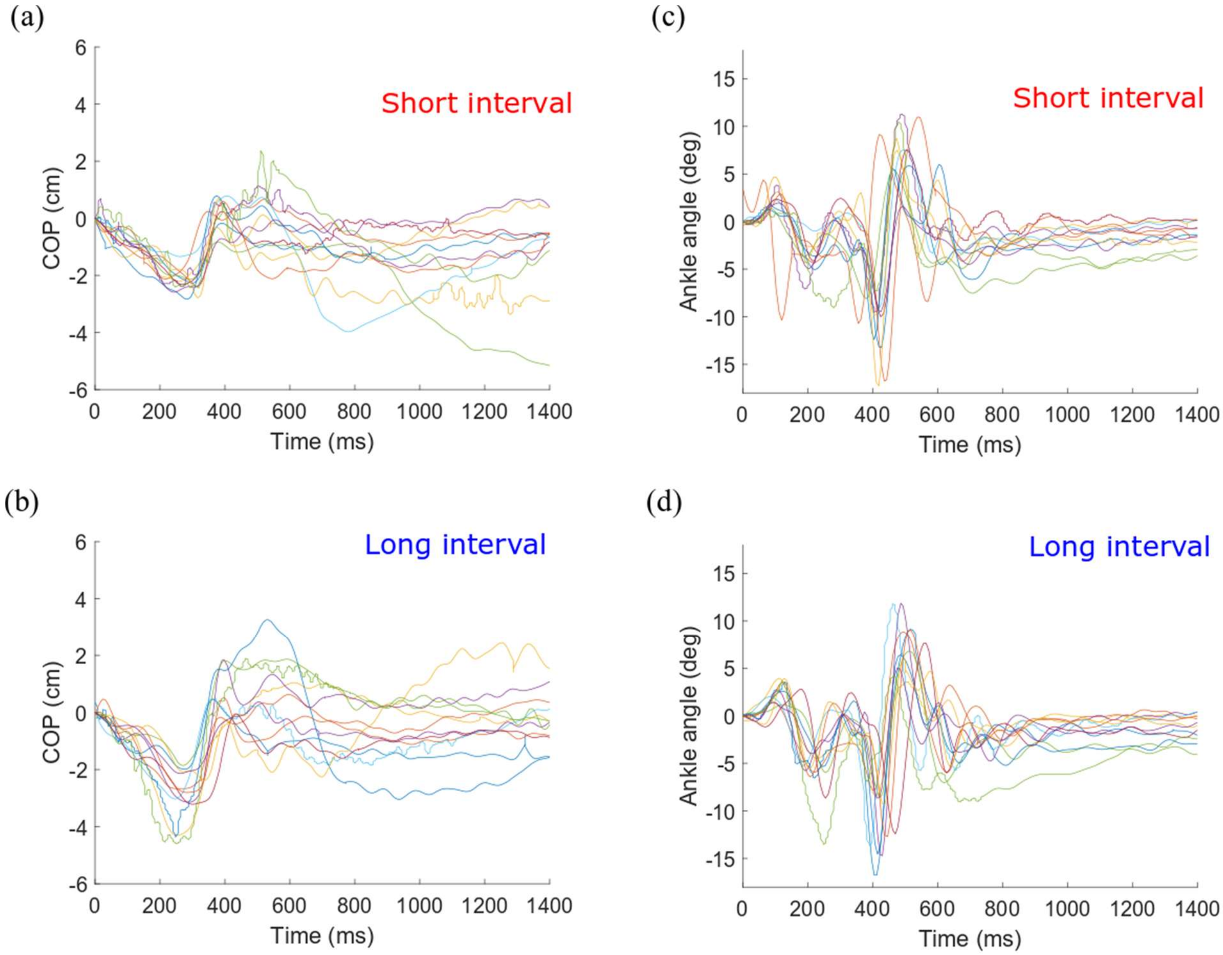

Fig 3. Traces of COP and ankle angle of individual participants at Trial 21 for Sequence 1 (longer interval) and Sequence 2 (shorter interval).