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Control of oscillatory force tasks: Low-frequency oscillations in force and muscle activity

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ABSTRACT

Force variability during steady force tasks is strongly related to low-frequency oscillations (< 0.25 Hz) in force. However, it is unknown whether low-frequency oscillations also contribute to the variability of oscillatory force tasks. To address this, twelve healthy young participants (21.08 ± 2.99 years, 6 females) performed a sinusoidal force task at 15% MVC at two different frequencies (0.5 and 1 Hz) with isometric abduction of the index finger. We recorded the force from the index finger and surface EMG from the first dorsal interosseous muscle and quantified the following outcomes: 1) trajectory variability and accuracy; 2) power spectrum of force and EMG bursting below 2 Hz; 3) power spectrum of the interference EMG from 4 to 60 Hz. The trajectory variability and error significantly increased from 0.5 to 1 Hz task ($P < 0.01$). Increased force oscillations < 0.25 Hz contributed to greater trajectory variability and error for both the 0.5 and 1 Hz oscillatory task ($R^2 > 0.33$; $P < 0.05$). The < 0.25 Hz oscillations in force were positively associated with greater power in the < 0.25 Hz for EMG bursting ($R^2 > 0.52$; $P < 0.01$). The modulation of the interference EMG from 35 to 60 Hz was a good predictor of the < 0.25 Hz force oscillations for both the 0.5 Hz task and 1 Hz task ($R^2 > 0.66$; $P < 0.01$). These results provide novel evidence that, similar to steady contractions, low-frequency oscillations of the motor neuron pool appear to be a significant mechanism that controls force during oscillatory force tasks.

1. Introduction

The force control scheme during isometric contractions appears to be the regulation of low-frequency oscillations in force (Lodha & Christou, 2017). Nonetheless, this is based on a specific case of isometric contractions, where the goal is to maintain a steady targeted force (steady force task). It remains unclear whether the Central Nervous System (CNS) uses the same control scheme when the goal is to oscillate the force output around a targeted force (oscillatory force task). This is an important question to address because the underlying physiology for force generation differs for the two isometric tasks. Here, we examine the contribution of low-frequency oscillations in force to the variability and accuracy of oscillatory force tasks and attempt to understand the underlying modulation of muscle activity.

During steady force contractions, low-frequency oscillations in force account for 50–80% of force variability (Fox et al., 2013; Lodha & Christou, 2017; Lodha, Misra, Coombes, Christou, & Cauraugh, 2013; Moon et al., 2014; Park, Casamento-Moran, Yacoubi, & Christou, 2017; Park, Kwon, & Christou, 2017). Experimental evidence suggests that these low-frequency oscillations are evident in single motor unit activity (Negro, Holobar, & Farina, 2009) and whole muscle activity as bursts in EMG (Moon et al., 2014; Park,

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Casamento-Moran et al., 2017; Park, Kwon et al., 2017; Yoshitake & Shinohara, 2013a). The current belief is that low-frequency oscillations in force are a consequence of central drive oscillations to the motor neuron pool. The work of Farina and colleagues (Farina & Negro, 2015; Negro et al., 2009) provide support to this hypothesis by demonstrating a strong association between the oscillations in force during steady contractions and the variability in estimated common input to motor neurons. Specifically, they suggest that the common input to the motor neuron pool includes low-frequency oscillations (Farina & Negro, 2015), which are transmitted to force oscillations (Negro et al., 2009). At the whole muscle level, there is evidence that oscillations in EMG bursting from 0 to 0.25 Hz contribute to low-frequency oscillations in force (Moon et al., 2014). Furthermore, there is evidence that the modulation of the interference EMG relates to the low-frequency oscillations in force and EMG bursting. Specifically, less 15–35 Hz power and more 35–60 Hz power in the interference EMG is associated with greater amplitude of low-frequency oscillations in the force output (Lodha & Christou, 2017; Moon et al., 2014). Therefore, low-frequency oscillations in force likely represent the modulation of the motor neuron pool by the central nervous system during steady isometric contractions.

Although low-frequency oscillations impair force control during steady force tasks (Fox et al., 2013; Lodha & Christou, 2017; Lodha et al., 2013; Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017), it remains unclear whether they contribute to the control of force during oscillatory force tasks. This is important because the underlying physiology for force generation differs for steady and oscillatory force tasks. During steady force tasks, the total muscle length, muscle fiber length, and tendon length remain relatively unchanged during the contraction (Aidley & Ashley, 1998; Bullock, Boyle, & Wang, 2001). In contrast, during the oscillatory force tasks, although the total muscle length remains relatively unchanged (isometric contractions), the muscle fiber length and tendon length varies with the phase of the oscillation (continuous alteration between force increase and decrease) (Fukunaga et al., 2001). Specifically, during force increase the muscle fibers shorten and the tendons lengthen, whereas during force decrease the muscle fibers lengthen and the tendons shorten. Therefore, oscillatory force tasks require the continuous recruitment and de-recruitment of motor units to vary force around the targeted force.

In this paper, we ask whether low-frequency oscillations in force and modulation of muscle activity also contribute to the control of oscillatory force tasks. To address this question, we asked participants to track a sinusoidal target at two different frequencies (0.5 and 1 Hz) with isometric abduction of the left index finger and examined their force and muscle activity modulation. Preliminary results have been presented in abstract form (Kim, Park, Paez, Moon, & Christou, 2015).

2. Materials and methods

2.1. Participants

Twelve young adults (21.08 ± 2.99 years, 6 females) volunteered for this study. All participants were healthy, moderately active, right-handed (Elias, Bryden, & Bulman-Fleming, 1998), and had normal or corrected vision. The Institutional Review Board at the University of Florida approved the procedures of this project and participants signed an informed consent.

2.2. Experimental protocol

Participants tracked a sinusoidal target at 15% MVC (amplitude: ± 7.5% MVC) at two different frequencies (0.5 and 1 Hz) with isometric abduction of the left index finger (oscillatory force tasks). We selected the left side because it was the non-dominant limb for each participant and, thus, there was more novelty to the task (Chen et al., 2012; Moon et al., 2014; Onushko, Baweja, & Christou, 2013; Park, Kwon, Solis, Lodha, & Christou, 2016). Each experimental session lasted ~ 1 h. Before the experimental session, we familiarized participants with the task and asked them to perform five practice trials with a light force at a different frequency from the actual task frequencies. After the familiarization period, each participant performed the following: 1) maximum voluntary contraction force (MVC) with abduction of the left index finger; 2) 0.5 and 1 Hz oscillatory force tasks (five trials each; counter-balanced order); and 3) repetition of the MVC task.

2.3. Experimental arrangement

2.3.1. Experimental setup and apparatus

The participants seated comfortably in an upright position and faced a 32-inch monitor (Samsung SyncMaster 275T+, Samsung Electronics America, NJ, USA) located 1.25 m away at eye level. The monitor displayed the target force (red line) and the force produced by the isometric abduction of the index finger (blue line) using a custom-written program in Matlab® (Math Works™ Inc., Natick, MA, USA). All participants affirmed that they could see the display clearly. Participants abducted the left arm 45° and flexed the elbow 90°. Using Velcro straps we secured the pronated left forearm on a customized metal plate and restrained the thumb, middle, ring, and little fingers of the left hand with metal plates. This arrangement allowed the isometric abduction of the index finger about the metacarpophalangeal joint in the horizontal plane (Fig. 1A), which is produced almost exclusively by the contraction of the first dorsal interosseous (FDI) muscle (Chao, An, Cooney, & Linscheid, 1989; Li & Yasuda, 2007).

2.3.2. Force measurement

We recorded the oscillatory force produced by the isometric abduction of the index finger with a one-dimensional force transducer (Futek LRF400 -FSH00263, capacity: 5 lb; Futek Advanced Sensor Technology Inc. CA, USA). We sampled the force signal at 1 kHz with a Power 1401 A/D board (Cambridge Electronic Design, UK) and a NI-DAQ card (Model USB6251, National Instruments, Austin,

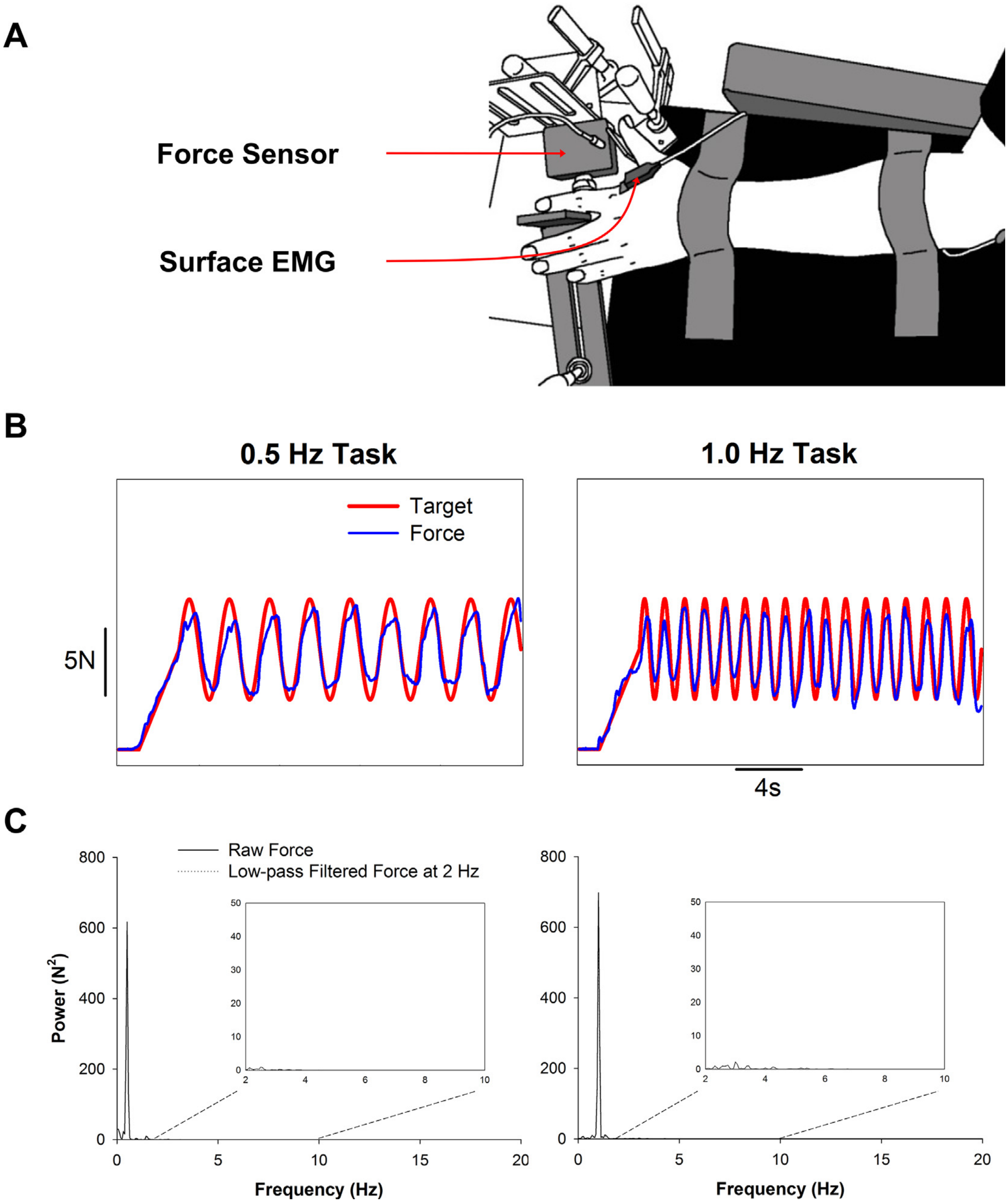

Fig. 1. Schematic of the experimental setup and oscillatory force task. A) Experimental setup. Participants placed the left index finger between a metal plate and a force sensor and performed isometric abduction of the left index finger. We recorded the force output and muscle activity from the FDI muscle. B) Representative data from one participant during the 0.5 Hz and 1 Hz tasks. The solid blue lines represent the force exerted by the participant, whereas the solid red lines represent the target force. C) Power spectrum of force (representative data from one participant; 0.5 Hz task – left; 1 Hz task - right). The solid lines represent the power spectrum of row force, whereas the dotted lines represent the power spectrum of low-passed filtered force at 2 Hz. Force below 2 Hz contains more than 95% of the raw force signal (0.5 Hz: 97.99 ± 2.14%; 1 Hz task: 95.41 ± 3.61%; total: 96.70 ± 3.23%).

TX, USA) and stored the data on a personal computer.

2.3.3. EMG measurement

We recorded the FDI muscle activity with a surface EMG electrode (Bagnoli TM, Single Differential, Delsys, Boston, MA, USA) that we taped on the skin distally to the innervation zone and in line with the muscle fibers (Homma & Sakai, 1991). We placed the reference electrode over the lateral epicondyle of the left humerus. We sampled the EMG signal at 1 kHz with a Power 1401 A/D board (Cambridge Electronic Design, UK) and a NI-DAQ card (Model USB6251, National Instruments, Austin, TX, USA). We amplified

(×1,000) and band-passed the EMG signal from 4 to 500 Hz (Bagnoli-16 Main Amplifier Unit, Delsys, Boston, MA, USA) and then stored it on a personal computer.

2.3.4. Maximum voluntary contraction (MVC) task

Participants increased abduction force of their index finger from baseline to the maximum over a 3 s period and then maintained the maximal force for 4 to 7 s. Each participant performed maximal trials until the maximum force of two trials was within 5% of each other. Participants had one minute of rest between trials. We used the average of the highest 3 s of force as the MVC. This procedure allowed for the identification of a more conservative MVC that reflects the capacity to maintain an isometric contraction. Participants repeated the MVC at the end of the experimental trials to determine whether muscle fatigue occurred.

2.3.5. Oscillatory force task

Each participant performed an oscillatory force task at two different frequencies (0.5 and 1 Hz). We counterbalanced the order of the oscillatory tasks across participants. We instructed participants to accurately and smoothly trace the sinusoidal target by abducting the left index finger. We displayed the sinusoidal target as a red line in the middle of the screen from left to right ranging from 7.5 to 22.5% MVC and a frequency of 0.5 and 1 Hz (Fig. 1B). We provided feedback of the participant's finger force as a blue line progressing in time from left to right across the monitor in real time (Fig. 1B). The gain of visual feedback remained constant at 5.4° throughout the experiment. For each task, participants performed 5 trials and each trial lasted 20 s. Participants had 1 min rest between trials and 3 min rest between the two tasks.

2.4. Data analysis

In this paper, we were interested in the low-frequency oscillations in force, which are associated with force variability (Fox et al., 2013; Lodha et al., 2013; Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017). Therefore, we focused on force oscillations below 0.25 Hz. We were also interested in low-frequency oscillations in EMG bursting and the modulation of the interference EMG because they are associated with low-frequency oscillations in force (Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017; Yoshitake & Shinohara, 2013a, 2013b). To achieve this, for every trial, we selected 16 s of force and EMG data that we analyzed off-line using a custom-written program in Matlab®.

2.4.1. Trajectory accuracy

We quantified trajectory accuracy with the root-mean-square error (RMSE) of the participant's raw force output relative to the target (Fig. 2A). In this paper, therefore, we use trajectory accuracy interchangeably with the RMSE or error.

2.4.2. Trajectory variability

We quantified trajectory variability by removing the task frequency. To remove the task frequency, we low-pass filtered the force signal at 2 Hz (second-order Butterworth) and applied a notch filter from 0.25 to 0.75 Hz for the 0.5 Hz task and from 0.75 to 1.25 Hz for the 1 Hz task (second-order Butterworth). We low-pass filter the force at 2 Hz because it contains more than 95% of the raw force signal (0.5 Hz: 97.99 ± 2.14%; 1 Hz task: 95.41 ± 3.61%; total: 96.70 ± 3.23%; Fig. 1C). We calculated the standard deviation (SD) of the detrended resultant force signal (Fig. 2A). In this paper, therefore, we use trajectory variability interchangeably with the SD of force.

2.4.3. Low-frequency oscillations in force

To remove the task frequency, we low-pass filtered the force signal at 2 Hz (second-order Butterworth) and applied a notch filter from 0.25 to 0.75 Hz for the 0.5 Hz task and from 0.75 to 1.25 Hz for the 1 Hz task (second-order Butterworth). To identify low-frequency oscillations in force we performed a Fourier analysis on the 16 s force signal (Christou, 2005) using a window size of 16 s (data length) that gave us a resolution of 0.063 Hz. Our interest in the force signal are low-frequency oscillations (< 0.25 Hz), thus, the dependent variable was the power from 0 to 0.25 Hz relative to the total power from 0 to 2 Hz (%) (right; Fig. 2A). We use force up to 2 Hz because it contains more than 95% of the raw force signal (0.5 Hz: 97.99 ± 2.14%; 1 Hz task: 95.41 ± 3.61%; total: 96.70 ± 3.23%; Fig. 1C).

2.4.4. Low-frequency oscillations in EMG bursting

To identify the bursting of the EMG signal we rectified (grey line; upper row; Fig. 2B) the interference EMG signal, low-pass filtered it at 2 Hz (black line; upper row; Fig. 2B; second-order Butterworth) and then detrended (black line; lower row; Fig. 2B) the low-pass filtered EMG signal (Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017). To remove the task frequency, we applied a notch filter from 0.25 to 0.75 Hz for the 0.5 Hz task and from 0.75 to 1.25 Hz for the 1 Hz task (second-order Butterworth). We performed a Fourier analysis on the EMG bursting using a window size of 16 s (data length) that gave us a resolution of 0.063 Hz. Our interest in this signal are low-frequency oscillations (< 0.25 Hz), thus, the dependent variable was the power from 0 to 0.25 Hz relative to the total power from 0 to 2 Hz (%) (right; Fig. 2B).

2.4.5. Interference EMG modulation

To identify the modulation of the EMG signal we performed a Fourier analysis on the raw detrended EMG signal using a window size of 16 s (data length) that gave us a resolution of 0.063 Hz. The dependent variables were the power from 4 to 7, 7–13, 13–35 and

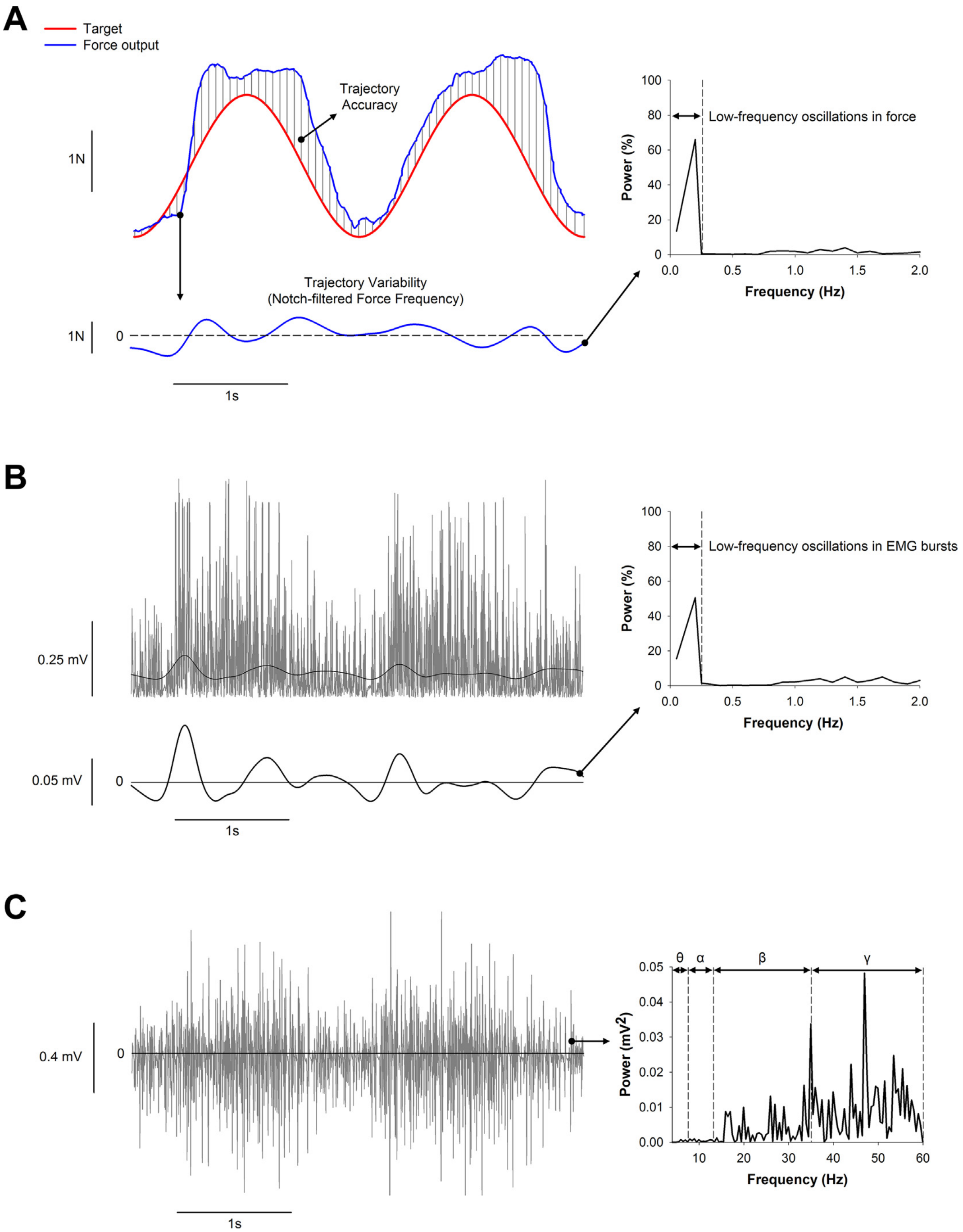

Fig. 2. Quantification of trajectory accuracy and variability, low-frequency oscillations in force and EMG bursting, and interference EMG modulation. A) We quantified accuracy with the root-mean-square error of the force output (upper row; blue line) from the target (upper row; red line). To quantify the trajectory variability, we low-pass filtered the force signal at 2 Hz and applied a notch filter and then calculated the SD of the detrended resultant force signal (lower row; blue line). We performed a power spectrum analysis on the processed force signal (right; representative data from one participant during the 0.5 Hz task). Our interest in the force signal was the power from 0 to 0.25 Hz relative to the total power from 0 to 2 Hz (%). B) We identified the EMG bursting by rectifying (upper row; grey line) the interference EMG, low-pass filtering the rectified EMG signal at 2 Hz (upper row; black line), and removing the task frequency and detrending the output (lower row). We performed a power spectrum analysis on the EMG bursting (right; representative data from one participant during the 0.5 Hz task). Our interest in the EMG bursts was the power from 0 to 0.25 Hz relative to the total power from 0 to 2 Hz (%). C) We identified the modulation of the EMG signal by performing a power spectrum analysis on the raw detrended EMG signal. The dependent variables were the power from 4 to 7 (theta band; θ), 7–13 (alpha band; α), 13–35 (beta band; β) and 35–60 (gamma band; γ) Hz relative to the total power from 4 to 60 Hz (%).

35–60 Hz relative to the total power from 4 to 60 Hz (%) (Park et al., 2016) (Fig. 2C).

2.5. Statistical analysis

We used a dependent *t*-test to compare mean force, SD of force, and RMSE in the 0.5 and 1 Hz task. We used linear regression models to determine the following: 1) the association between the SD of force and power from 0 to 0.25 Hz in the force output; 2) the association between the RMSE and power from 0 to 0.25 Hz in the force output; 3) the association between the power from 0 to 0.25 Hz in the force output and the power from 0 to 0.25 Hz in the EMG bursting; 4) the association between the power from 0 to 0.25 Hz in the force output and the power from 4 to 60 Hz in the interference EMG. We used a stepwise multiple linear regression model to predict the low frequency oscillations in force from the modulation of the interference EMG (4–7, 7–13, 13–35, & 35–60 Hz as independent variables). The goodness-of-fit of the model was given by the squared multiple correlations (R^2), Durbin Watson statistic (DW), and part correlation coefficients that demonstrate the unique contribution of each predictor to the criterion variable. Analyses were performed with the IBM SPSS Statistics 25.0 statistical package (IBM Corp., Armonk, NY, USA). The alpha level for all statistical tests was 0.05, which was corrected for multiple comparisons. Data are reported as mean ± SD in the text and mean ± standard error of the mean in the figures.

3. Results

3.1. Low-frequency oscillations in force

Our primary goal was to determine whether low-frequency oscillations in force (< 0.25 Hz) contribute to trajectory variability

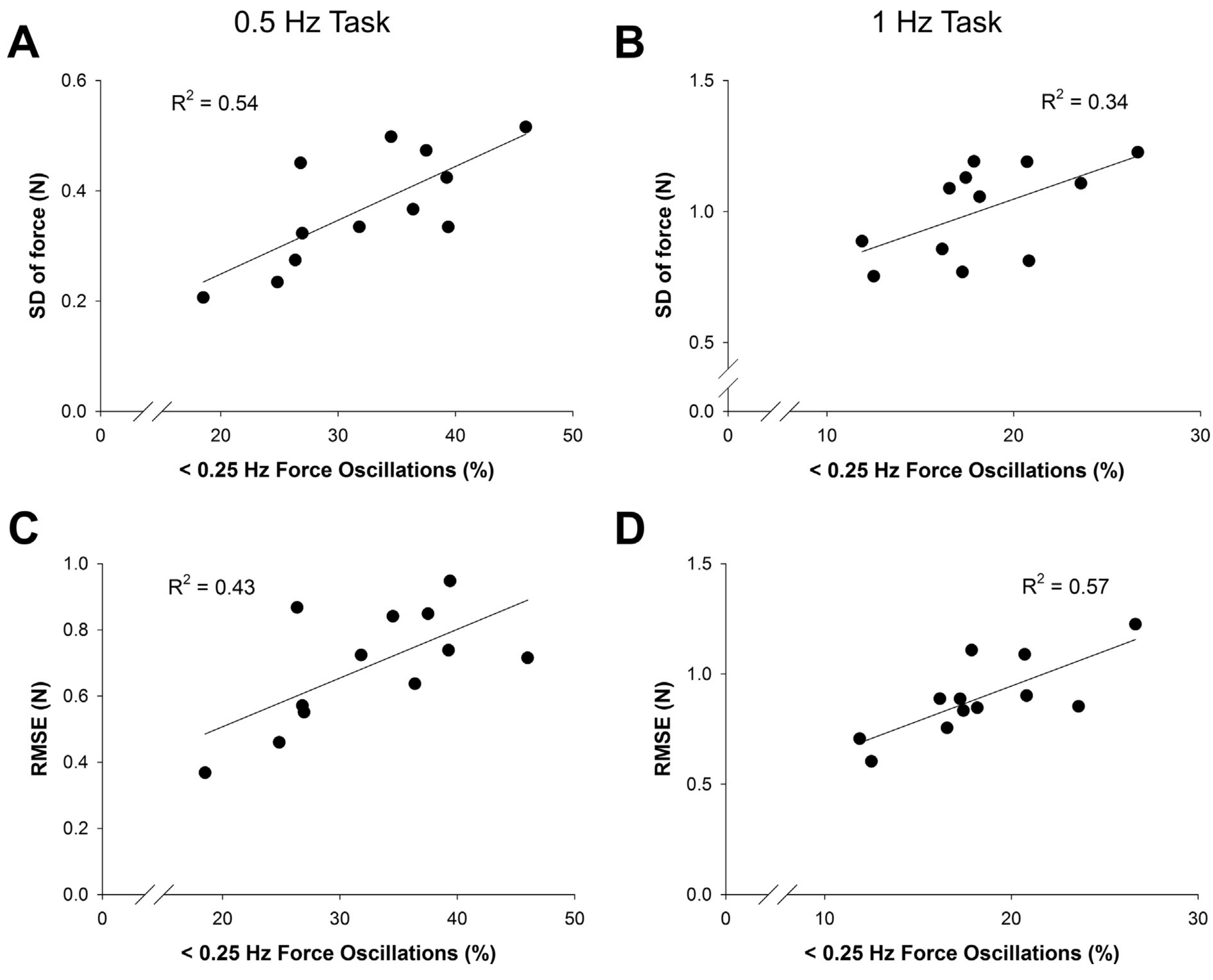

Fig. 3. Performance and low-frequency oscillations in force. A) During the 0.5 Hz task, ~54% of trajectory variability was associated with force oscillations from 0 to 0.25 Hz ($P < 0.01$). B) During the 1 Hz task, ~34% of trajectory variability was associated with force oscillations from 0 to 0.25 Hz ($P < 0.05$). C) During the 0.5 Hz task, ~43% of error was associated with force oscillations from 0 to 0.25 Hz ($P < 0.03$). D) During the 1 Hz task, ~57% of error was associated with force oscillations from 0 to 0.25 Hz ($P < 0.01$).

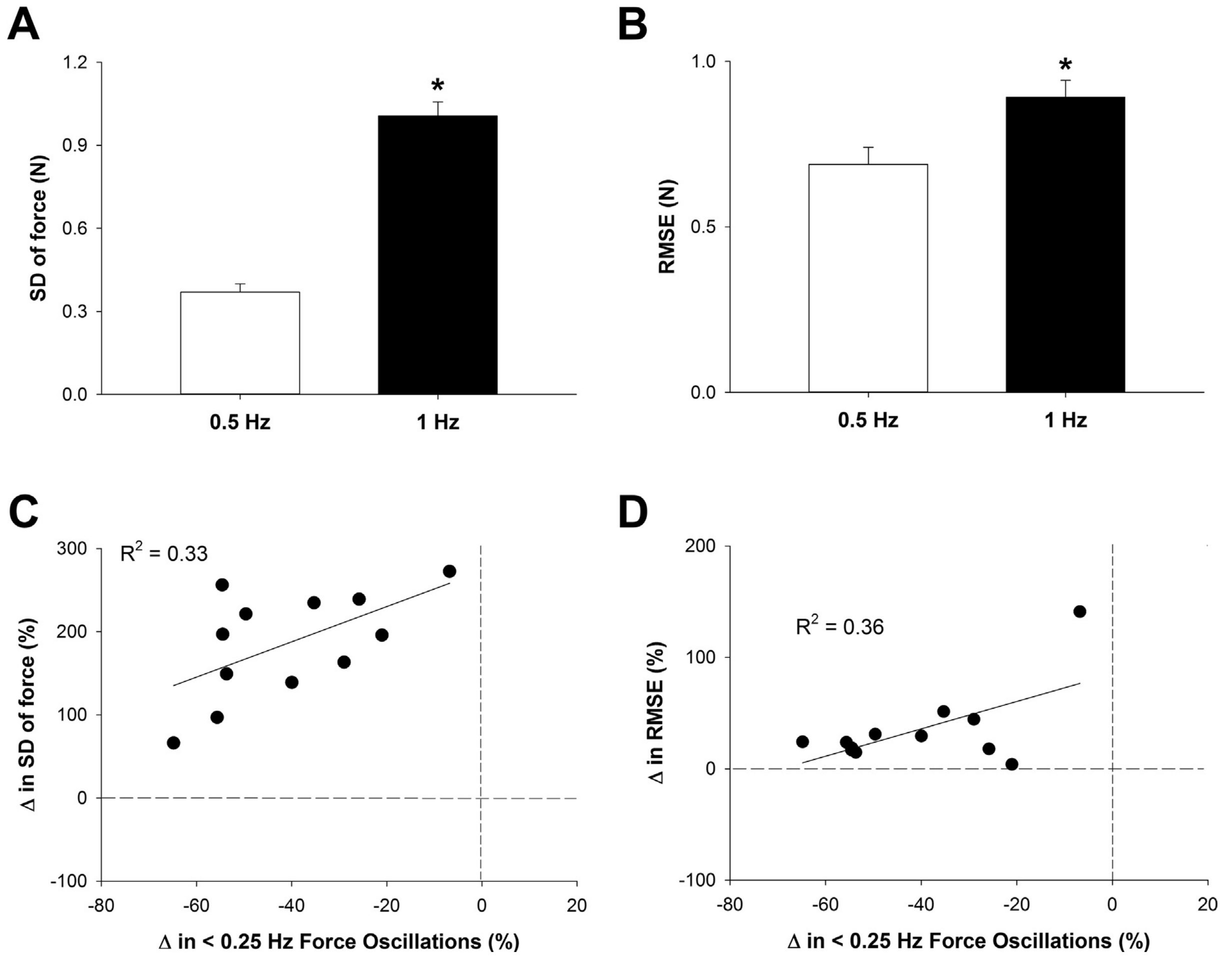

Fig. 4. Change in performance and low-frequency oscillations in force. A) Trajectory variability significantly increased with task frequency ($P < 0.01$). B) Error significantly increased with task frequency ($P < 0.01$). C) The increase in trajectory variability from the 0.5 to 1 Hz task was associated with the increase in the power of force oscillations from 0 to 0.25 Hz ($R^2 = 0.33$). D) The increase in error from the 0.5 to 1 Hz task was associated with the increase in the power of force oscillations from 0 to 0.25 Hz ($R^2 = 0.36$).

and error during oscillatory tasks performed at two different frequencies (0.5 and 1 Hz). There was a significant positive association between the trajectory variability and < 0.25 Hz oscillations in force for both tasks [0.5 Hz task ($R^2 = 0.54$, DW = 1.79, $P < 0.01$; Fig. 3A) and 1 Hz task ($R^2 = 0.34$, DW = 1.66, $P < 0.05$; Fig. 3B)]. There was also a significant positive association between the trajectory error and < 0.25 Hz oscillations in force for both tasks [0.5 Hz task ($R^2 = 0.43$, DW = 2.33, $P < 0.03$; Fig. 3C) and 1 Hz task ($R^2 = 0.57$, DW = 1.76, $P < 0.01$; Fig. 3D)].

To determine whether low-frequency oscillations in force could explain the change in performance during oscillatory tasks we examined the difference in force variability and error for the two tasks. The trajectory variability (t = -13.90, $P < 0.01$; Fig. 4A) and error (t = -5.21, $P < 0.01$; Fig. 4B) significantly increased with task frequency. The increase in trajectory variability ($R^2 = 0.33$, DW = 1.11, $P < 0.05$; Fig. 4C) and error ($R^2 = 0.36$, DW = 2.23, $P < 0.05$; Fig. 4D) with task frequency was significantly related to an increase in power for the < 0.25 Hz force oscillations.

3.2. Low-frequency oscillations in EMG bursting

Based on previous findings, we expected the low-frequency oscillations in force to correlate with low-frequency oscillations in EMG bursting. To achieve this, we examined the association between the power < 0.25 Hz in force and the power < 0.25 Hz in the EMG bursting for the two oscillatory tasks. We found a significant positive association between the force and EMG bursting oscillations < 0.25 Hz for both tasks [0.5 Hz task ($R^2 = 0.52$, DW = 1.86, $P < 0.01$; Fig. 5A) and 1 Hz task ($R^2 = 0.63$, DW = 2.47, $P < 0.01$; Fig. 5B)]. The increase in power for the < 0.25 Hz force oscillations with task frequency was significantly related to an increase in power for the < 0.25 Hz EMG bursting ($R^2 = 0.75$, DW = 2.03, $P < 0.01$; Fig. 5C).

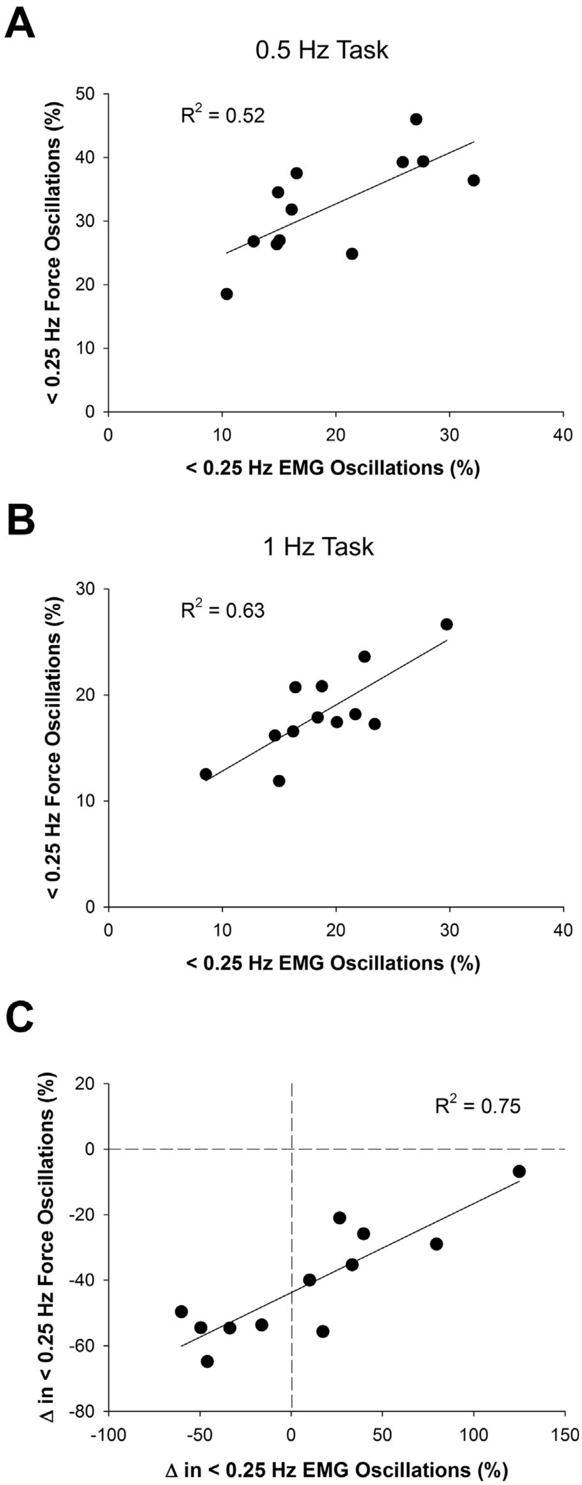

Fig. 5. Low-frequency oscillations in force and EMG bursts. A) During the 0.5 Hz task, ~52% of force oscillations from 0 to 0.25 Hz was correlated to EMG burst oscillations from 0 to 0.25 Hz ($P < 0.01$). B) During the 1 Hz task, ~63% of force oscillations from 0 to 0.25 Hz was correlated to EMG burst oscillations from 0 to 0.25 Hz ($P < 0.01$). C) The increase in < 0.25 Hz force oscillations from the 0.5 to 1 Hz task was significantly associated with the increase in < 0.25 Hz EMG burst oscillations ($R^2 = 0.75$).

3.3. Modulation of interference EMG

Another interest of this study was to examine whether modulation of the interference EMG from 4 to 60 Hz could predict the low-frequency oscillations in force. To achieve this, we examined whether a stepwise linear regression model could predict low-frequency oscillations in force (dependent variable) from the modulation of the interference EMG at different bands (4–7, 7–13, 13–35, and 35–60 Hz; independent variables).

We found that the modulation of the interference EMG from 35 to 60 Hz was a good predictor of the < 0.25 Hz force oscillations for both the 0.5 Hz task and 1 Hz task. For the 0.5 Hz task greater < 0.25 Hz force oscillations were significantly predicted from less power within 7–13 Hz and greater power within 35–60 Hz of the interference EMG ($R^2 = 0.83$, DW = 1.74, $P < 0.01$; Fig. 6A). For the 1 Hz task greater < 0.25 Hz force oscillations were significantly predicted from greater power within 35–60 Hz of the interference EMG ($R^2 = 0.66$, DW = 2.50, $P < 0.01$; Fig. 6B). The increase in < 0.25 Hz force oscillations with task frequency was significantly associated with the increase in power within 35–60 Hz of the interference EMG ($R^2 = 0.77$, DW = 1.28, $P < 0.01$; Fig. 6C).

4. Discussion

In this study, we aimed to determine whether low-frequency oscillations in force relate to the variability and accuracy of oscillatory force tasks. Similar to steady force contractions, we found that force oscillations < 0.25 Hz contributed significantly to trajectory variability and accuracy during oscillatory force contractions. The force oscillations < 0.25 Hz correlated with EMG bursting < 0.25 Hz and with more power from 35 to 60 Hz in the interference EMG. To our knowledge, this is the first paper that provides evidence that low-frequency oscillations in force contribute significantly to oscillatory force control.

4.1. Low-frequency oscillations in force

In this study, we found that low-frequency oscillations in force contribute significantly to the trajectory variability of oscillatory force tasks. Specifically, the power of the force spectra < 0.25 Hz related to the SD of force during the oscillatory tasks. This supports numerous studies on steady contractions (Fox et al., 2013; Lodha & Christou, 2017; Lodha et al., 2013; Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017) and extends the findings to oscillatory contractions. The contribution of low-frequency oscillations to the oscillatory force tasks was lower than that for the steady force tasks (~30–50% vs. 50–80%). Regardless of the magnitude of the contribution, our findings demonstrate that low-frequency oscillations in force are also relevant to oscillatory force control.

The importance of reducing low-frequency oscillations in force to enhance force control is demonstrated in recent studies. Specifically, we recently published an acute intervention where we decreased force variability of steady contractions in healthy young adults by providing them with visual constraints (Park, Casamento-Moran et al., 2017). Most importantly, we found that participants reduced their force variability by decreasing the amplitude of low-frequency oscillations in force (Park, Casamento-Moran et al., 2017). Support to this finding comes from a longer intervention in stroke, where following precision training the improvement in force control of the paretic hand was associated with a decrease in low-frequency oscillations in the force output (Kang & Cauraugh, 2014). Overall, these two findings suggest that low-frequency oscillations are a critical motor output variable that the central nervous system must control.

4.2. EMG bursting

We also found that the oscillations in force < 0.25 Hz during oscillatory force contractions related positively to the oscillations in the EMG bursting < 0.25 Hz. This supports recent findings in studies that used steady contractions and found an association between low-frequency oscillations in force and EMG bursting (Lodha et al., 2013; Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017). In addition, this finding supports the work of Farina and colleagues (Farina & Negro, 2015; Negro et al., 2009) who propose the following: 1) Only the low-frequency oscillations to the motor neuron pool by the common drive are transformed into the force output oscillations; 2) The low-frequency oscillations of the motor neuron pool account for most of force oscillations. The low-frequency oscillations observed in EMG bursting, therefore, likely represent the modulation of the motor neuron pool from the central drive.

It is possible that low-frequency oscillations in muscle activity reflect a CNS strategy to control the numerous active spinal motor neurons. Instead of controlling individual spinal motor neurons, the CNS groups the activity of the spinal motor neurons into low-frequency units. This provides the CNS with a solution to the degrees of freedom problem (Bernstein, 1967) and an efficient way to regulate force output (Latash, 2012; Lodha & Christou, 2017). This is supported by recent findings where the reduction in low-frequency oscillations in force is associated with a reduction of the low-frequency oscillations in EMG bursting (Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017).

4.3. Interference EMG modulation and low-frequency oscillations

There is evidence that the brain communicates with the spinal motor neuron pool primarily through beta (13–35 Hz) and gamma band (35–60 Hz) oscillations (Baker, Kilner, Pinches, & Lemon, 1999; Conway et al., 1995; Halliday, Conway, Farmer, & Rosenberg, 1998; Kilner et al., 1999; Kristeva-Feige, Fritsch, Timmer, & Lücking, 2002; Kristeva, Patino, & Omlor, 2007). Thus, another interest

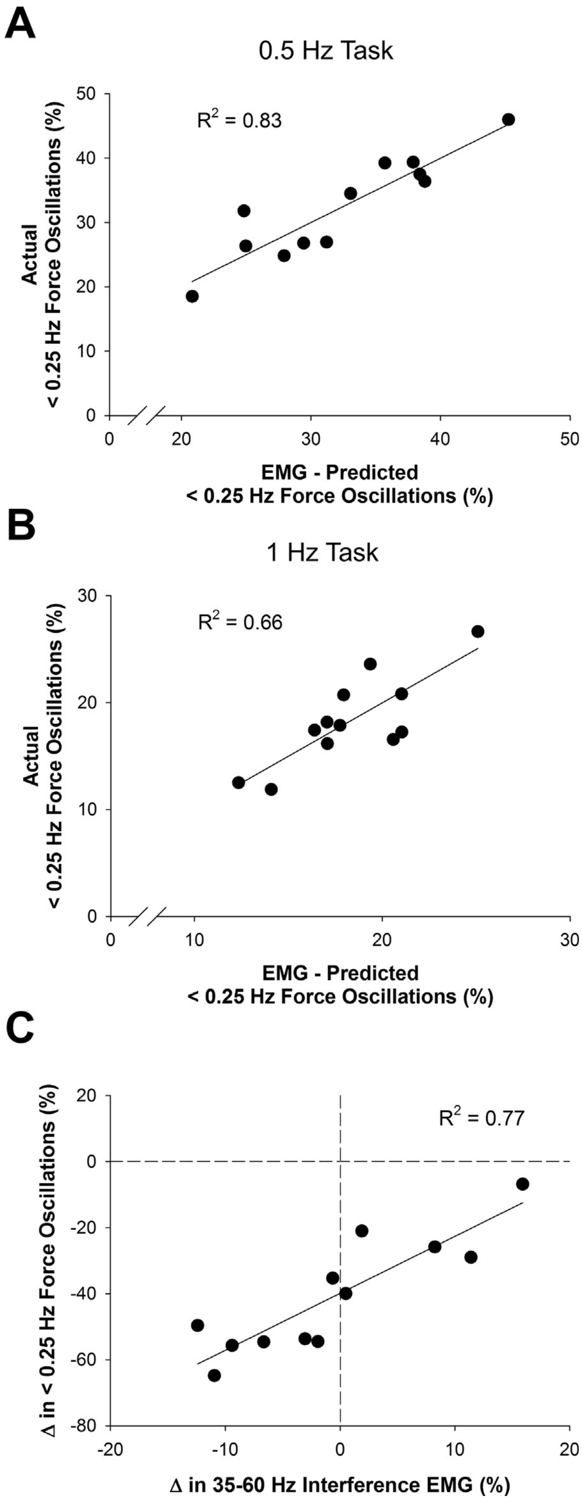

Fig. 6. Low-frequency oscillations in force predicted from the interference EMG. A) During the 0.5 Hz task, ~83% of force oscillations from 0 to 0.25 Hz were predicted from the interference EMG from 7 to 13 and 35–60 Hz ($P < 0.01$). B) During the 1 Hz task, ~66% of force oscillations from 0 to 0.25 Hz were predicted from the interference EMG from 35 to 60 Hz ($P < 0.01$). C) The increase in < 0.25 Hz force oscillations from the 0.5 to 1 Hz task was significantly associated with the increase in power within 35–60 Hz of the interference EMG ($R^2 = 0.77$).

of this study was to examine whether modulation of the interference EMG from 4 to 60 Hz could predict the low-frequency oscillations in force during oscillatory force tasks. Power from 35 to 60 Hz, termed gamma band (Berger, 1930), is related to sensorimotor integration (Brown, 2003) and movement preparation and execution (Donner, Siegel, Fries, & Engel, 2009; Schoffelen, Oostenveld, & Fries, 2005). The gamma band is considered “pro-kinetic” because the neural activity occurs at the gamma band during the preparation and execution of voluntary movements (Donner et al., 2009; Schoffelen et al., 2005). In this study, we found that greater power in the gamma band of the interference EMG results in greater low-frequency force oscillations. In support to recent findings (Moon et al., 2014; Park, Casamento-Moran et al., 2017; Park, Kwon et al., 2017), we demonstrate that greater gamma band oscillations to the motor neuron pool, as evidenced in the interference EMG, increase the amplitude of low-frequency oscillations of force. This amplification of low-frequency force oscillations results in greater trajectory variability.

An alternative mechanism is to increase the beta band oscillations to the motor neuron pool. Power from 13 to 35 Hz, termed beta band (Berger, 1930), is considered “anti-kinetic” (Engel and Fries 2010). Numerous experiments suggest that when the brain is activated at that frequency, the force output is steadier. For example, the beta band oscillations are particularly pronounced during steady contractions but attenuated by voluntary movements (Baker et al., 1999; Conway et al., 1995; Halliday et al., 1998; Kilner et al., 1999; Kristeva et al., 2007). Indeed, we found that participants during the 0.5 Hz oscillatory task (steadier) exhibited lesser beta EMG power (t = -2.30; $P < 0.05$). Therefore, it appears that a downregulation of the beta band and an upregulation of the gamma band modulation of the spinal motor neuron pool increase low-frequency oscillations in force.

5. Limitations

Our findings are limited to task frequencies of 0.5 and 1 Hz and to a force of 15% MVC. Future studies should perform similar experiments but manipulate the task frequencies and level of force, and perform similar experiments with movements. In addition, because our participants were limited to healthy young adults, it is not clear whether our findings will generalize to other populations with greater force variability such as children (Deutsch & Newell, 2001), older adults (Fox et al., 2013; Kennedy & Christou, 2011; Park, Kwon et al., 2017), or adults with neurological disorders (Casamento Moran et al., 2015; Cleeves & Findley, 1987; Lodha et al., 2013; Shakkottai et al., 2011). Finally, the current muscle activity findings are based on recordings with surface EMG. Future studies should verify these results using intramuscular recordings, which are not limited to the skin conductance issues (Christou, Rudroff, Enoka, Meyer, & Enoka, 2007; Galganski, Fuglevand, & Enoka, 1993).

6. Conclusion

In summary, our results extend current literature which suggests that greater low-frequency oscillations in force are detrimental to force control. Previous studies drew these conclusions using steady force contractions. Here, to our knowledge, we present the first evidence that greater low-frequency oscillations in force are also detrimental to oscillatory force control. Similar to steady contractions we provide evidence that an upregulation of the spinal motor neuron pool modulation in the gamma band results in greater low-frequency oscillations in EMG bursting and force output. Therefore, mechanisms of force control, namely low-frequency oscillations of the motor neuron pool, likely control force during steady and oscillatory contractions.

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References

Aidley, D. J., & Ashley, D. (1998). *The physiology of excitable cells.* Cambridge: Cambridge University Press.
Baker, S., Kilner, J., Pinches, E., & Lemon, R. (1999). The role of synchrony and oscillations in the motor output. *Experimental Brain Research, 128*, 109–117.
Berger, H. (1930). Electroencephalogram of humans. *Journal fur Psychologie und Neurologie, 40*, 160–179.
Bernstein, N. (1967). *The coordination and regulation of movements.* Oxford: Pergamon Press.
Brown, P. (2003). Oscillatory nature of human basal ganglia activity: Relationship to the pathophysiology of Parkinson's disease. *Movement Disorders, 18*, 357–363.
Bullock, J., Boyle, J., III, & Wang, M. B. (2001). NMS physiology (national medical series for independent study). *Lippincott Williams and Wilkins.*.
Casamento Moran, A., Chen, Y.-T., Kwon, M., Snyder, A., Subramony, S., Vaillancourt, D., & Christou, E. A. (2015). Force dysmetria in spinocerebellar ataxia 6 correlates with functional capacity. *Frontiers in Human Neuroscience, 9*, 184.
Chao, E. Y., An, K.-N., Cooney, W. P., III, & Linscheid, R. L. (1989). *Biomechanics of the hand: A basic research study.* World Scientific.
Chen, Y.-T., Neto, O. P., de Miranda Marzullo, A. C., Kennedy, D. M., Fox, E. J., & Christou, E. A. (2012). Age-associated impairement in endpoint accuracy of goal-directed contractions performed with two fingers is due to altered activation of the synergistic muscles. *Experimental Gerontology, 47*, 519–526.
Christou, E. A. (2005). Visual feedback attenuates force fluctuations induced by a stressor. *Medicine and Science in Sports and Exercise, 37*, 2126–2133.
Christou, E. A., Rudroff, T., Enoka, J. A., Meyer, F., & Enoka, R. M. (2007). Discharge rate during low-force isometric contractions influences motor unit coherence below 15 Hz but not motor unit synchronization. *Experimental Brain Research, 178*, 285–295.
Cleeves, L., & Findley, L. J. (1987). Variability in amplitude of untreated essential tremor. *Journal of Neurology, Neurosurgery and Psychiatry, 50*, 704–708.
Conway, B., Halliday, D., Farmer, S., Shahani, U., Maas, P., Weir, A., & Rosenberg, J. (1995). Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man. *The Journal of Physiology, 489*, 917–924.
Deutsch, K. M., & Newell, K. M. (2001). Age differences in noise and variability of isometric force production. *Journal of Experimental Child Psychology, 80*, 392–408.
Donner, T. H., Siegel, M., Fries, P., & Engel, A. K. (2009). Buildup of choice-predictive activity in human motor cortex during perceptual decision making. *Current Biology, 19*, 1581–1585.
Elias, L. J., Bryden, M. P., & Bulman-Fleming, M. B. (1998). Footedness is a better predictor than is handedness of emotional lateralization. *Neuropsychologia, 36*, 37–43.
Farina, D., & Negro, F. (2015). Common synaptic input to motor neurons, motor unit synchronization, and force control. *Exercise and Sport Sciences Reviews, 43*, 23–33.

Fox, E. J., Baweja, H. S., Kim, C., Kennedy, D. M., Vaillancourt, D. E., & Christou, E. A. (2013). Modulation of force below 1 Hz: Age-associated differences and the effect of magnified visual feedback. *PLoS One, 8*, e55970.

Fukunaga, T., Kubo, K., Kawakami, Y., Fukashiro, S., Kanehisa, H., & Maganaris, C. N. (2001). In vivo behaviour of human muscle tendon during walking. *Proceedings of the Royal Society of London B: Biological Sciences, 268*, 229–233.

Galganski, M. E., Fuglevand, A. J., & Enoka, R. M. (1993). Reduced control of motor output in a human hand muscle of elderly subjects during submaximal contractions. *Journal of Neurophysiology, 69*, 2108–2115.

Halliday, D. M., Conway, B. A., Farmer, S. F., & Rosenberg, J. R. (1998). Using electroencephalography to study functional coupling between cortical activity and electromyograms during voluntary contractions in humans. *Neuroscience Letters, 241*, 5–8.

Homma, T., & Sakai, T. (1991). Ramification pattern of intermetacarpal branches of the deep branch (ramus profundus) of the ulnar nerve in the human hand. *Cells, Tissues, Organs, 141*, 139–144.

Kang, N., & Cauraugh, J. H. (2014). Force control improvements in chronic stroke: Bimanual coordination and motor synergy evidence after coupled bimanual movement training. *Experimental Brain Research, 232*, 503–513.

Kennedy, D. M., & Christou, E. A. (2011). Greater amount of visual information exacerbates force control in older adults during constant isometric contractions. *Experimental Brain Research, 213*, 351–361.

Kilner, J., Baker, S., Salenius, S., Jousmäki, V., Hari, R., & Lemon, R. (1999). Task-dependent modulation of 15–30 Hz coherence between rectified EMGs from human hand and forearm muscles. *The Journal of physiology, 516*, 559–570.

Kim, C., Park, S. H., Paez, C., Moon, H., & Christou, E. A. (2015). Low-frequency oscillations in force and muscle activity relate to force variability during sinusoidal tasks. In Society for the Neural Control of Movement Annual Meeting. Charleston.

Kristeva-Feige, R., Fritsch, C., Timmer, J., & Lücking, C.-H. (2002). Effects of attention and precision of exerted force on beta range EEG-EMG synchronization during a maintained motor contraction task. *Clinical Neurophysiology, 113*, 124–131.

Kristeva, R., Patino, L., & Omlor, W. (2007). Beta-range cortical motor spectral power and corticomuscular coherence as a mechanism for effective corticospinal interaction during steady-state motor output. *Neuroimage, 36*, 785–792.

Latash, M. L. (2012). The bliss (not the problem) of motor abundance (not redundancy). *Experimental Brain Research, 217*, 1–5.

Li, S., & Yasuda, N. (2007). Forced ventilation increases variability of isometric finger forces. *Neuroscience Letters, 412*, 243–247.

Lodha, N., & Christou, E. A. (2017). Low-frequency oscillations and control of the motor output. *Frontiers in Physiology,* 8.

Lodha, N., Misra, G., Coombes, S. A., Christou, E. A., & Cauraugh, J. H. (2013). Increased force variability in chronic stroke: Contributions of force modulation below 1 Hz. *PLoS One, 8*, e83468.

Moon, H., Kim, C., Kwon, M., Chen, Y. T., Onushko, T., Lodha, N., & Christou, E. A. (2014). Force control is related to low-frequency oscillations in force and surface EMG. *PLoS One, 9*, e109202.

Negro, F., Holobar, A., & Farina, D. (2009). Fluctuations in isometric muscle force can be described by one linear projection of low-frequency components of motor unit discharge rates. *The Journal of physiology, 587*, 5925–5938.

Onushko, T., Baweja, H. S., & Christou, E. A. (2013). Practice improves motor control in older adults by increasing the motor unit modulation from 13 to 30 Hz. *Journal of Neurophysiology, 110*, 2393–2401.

Park, S. H., Casamento-Moran, A., Yacoubi, B., & Christou, E. A. (2017). Voluntary reduction of force variability via modulation of low-frequency oscillations. *Experimental Brain Research, 235*, 2717–2727.

Park, S. H., Kwon, M., & Christou, E. A. (2017). Motor output oscillations with magnification of visual feedback in older adults. *Neuroscience Letters, 647*, 8–13.

Park, S. H., Kwon, M., Solis, D., Lodha, N., & Christou, E. A. (2016). Motor control differs for increasing and releasing force. *Journal of Neurophysiology, 115*, 2924–2930.

Schoffelen, J.-M., Oostenveld, R., & Fries, P. (2005). Neuronal coherence as a mechanism of effective corticospinal interaction. *Science, 308*, 111–113.

Shakkottai, V. G., do Carmo Costa, M., Dell'Orco, J. M., Sankaranarayanan, A., Wulff, H., & Paulson, H. L. (2011). Early changes in cerebellar physiology accompany motor dysfunction in the polyglutamine disease spinocerebellar ataxia type 3. *The Journal of Neuroscience, 31*, 13002–13014.

Yoshitake, Y., & Shinohara, M. (2013a). Low-frequency component of rectified EMG is temporally correlated with force and instantaneous rate of force fluctuations during steady contractions. *Muscle and Nerve, 47*, 577–584.

Yoshitake, Y., & Shinohara, M. (2013b). Oscillations in motor unit discharge are reflected in the low-frequency component of rectified surface EMG and the rate of change in force. *Experimental Brain Research, 231*, 267–276.