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SPEED, RESISTANCE, AND UNEXPECTED ACCELERATIONS MODULATE FEED FORWARD AND FEEDBACK CONTROL DURING A NOVEL WEIGHT BEARING TASK

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Abstract

We developed a method to investigate feed-forward and feedback movement control during a weight bearing visuomotor knee tracking task. We hypothesized that a systematic increase in speed and resistance would show a linear decrease in movement accuracy, while unexpected perturbations would induce a velocity-dependent decrease in movement accuracy. We determined the effects of manipulating the speed, resistance, and unexpected events on error during a functional weight bearing task. Our long term objective is to benchmark neuromuscular control performance across various groups based on age, injury, disease, rehabilitation status, and/or training. Twenty-six healthy adults between the ages of 19–45 participated in this study. The study involved a single session using a custom designed apparatus to perform a single limb weight bearing task under nine testing conditions: three movement speeds (0.2, 0.4, and 0.6 Hz) in combination with three levels of brake resistance (5%, 10%, and 15% of individual's body weight). Individuals were to perform the task according to a target with a fixed trajectory across all speeds, corresponding to a ~ 0 (extension) to 30 degrees (flexion) of knee motion. An increase in error occurred with speed ($p < 0.0001$, effect size (η^2): $\eta^2 = 0.50$) and resistance ($p < 0.0001$, $\eta^2 = 0.01$). Likewise, during unexpected perturbations, the ratio of perturbed/non-perturbed error increased with each increment in velocity ($p < .0014$, $\eta^2 = 0.08$), and resistance ($p < .0001$, $\eta^2 = 0.11$). The hierarchical framework of these measurements offers a standardized functional weight bearing strategy to assess impaired neuro-muscular control and/or test the efficacy of therapeutic rehabilitation interventions designed to influence neuromuscular control of the knee.

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Keywords

feedback; long-latency reflex; neuromuscular control; visuomotor; force perturbation

INTRODUCTION

Feed-forward and feedback movement strategies are fundamental to optimal neuromuscular control in humans [1, 2]. Altered neuromuscular control is associated with poor human performance across the spectrum of function: from elite athletes falling short of a record to the person with Parkinson's disease unable to ambulate a short distance to be independent. Typically, injury occurs when the central nervous system is fooled with an event that was not expected, relying entirely on a feedback response. The integration of the anticipatory commands and the feedback commands is well documented; however, our understanding of feed-forward and feedback control during functional weight bearing movements remains elusive. In this study we assess the effects of manipulating the speed, resistance, and unexpected events on error during a novel functional weight bearing task.

While there is limited information on how speed and resistance cause the CNS to scale neuromuscular responses during weight bearing tasks, there are rich resources guiding us from the upper extremity literature. Feed-forward control of the upper extremity reflects the open-loop plan of movement, and has been shown to decrease in accuracy with increase in speed [1, 3, 4], and resistance [5, 6]. Feedback control, however, is the closed-loop, error driven change in movement. Reaching experiments have provided evidence that unexpected acceleration/deceleration induced by mid-movement changes in speed [7, 8] and resistance [9, 10], also diminish movement accuracy. Because whole body unexpected events involve the vestibular, visual, and somatosensory systems, the findings may vary from reports for upper extremity perturbations.

Our initial investigation of a single limb squat as a visuomotor task revealed that a fixed level of difficulty modulates the feed-forward and feedback control strategies as supported by changes in muscle activity about the knee. Improvements in performance can be achieved even under conditions where a person is denied visual feedback [11, 12], is fatigued [13], older [14], or post-surgical [15, 16]. A limitation of our previous reports is that only a single level of resistance and speed was assessed during the weight bearing task, suggesting that the assessment would show ceiling or floor effects in other populations.

During routine clinical assessment we typically measure impairments with a vast range of techniques (e.g. muscle testing, gross motor function exams, range of motion testing, sensory testing, timed standing balance, coordination, reflexes, and quality and endurance of gait). Testing how healthy people scale lower extremity movement and perturbation responses during a range of difficulty will provide insights into control of weight bearing functional movement. We believe that this is important in order to assess the integration of movement systems and strategies, and may provide a rapid method to characterize impairment, and, presumably, disability.

The purpose of this study was to determine if changes in speed, resistance, and unexpected acceleration either independently or in combination leads to reduced movement accuracy in a hierarchical pattern (greater error with greater resistance and/or greater speed). We hypothesize that an increase in speed and resistance would yield a linear decrease in movement accuracy, while unexpected perturbations would lead to a velocity-dependent and resistance dependent decrease in movement accuracy.

METHODS

Subjects

A total of 26 healthy adults aged 19 – 45 years (mean(SD), 27.7(6.7) years; nine females and seventeen males) participated in the study. All subjects enrolled in the study had no acute or ongoing orthopedic, neuromuscular, or neurological deficits or disorders. Each individual gave informed consent before participation and our institution's Human Subjects Institutional Review Board approved the study.

Paradigm

The study involved a single session using a previously developed therapeutic exercise system [17] to deliver nine testing conditions: three movement speeds (0.2, 0.4, and 0.6 Hz) in combination with three levels of brake resistance (5%, 10%, and 15% of individual's body weight). Only the dominant leg was tested, as was defined as the side with which one would kick a ball. Each testing condition was separated by a one-minute rest period. The order of testing condition is fixed across all subjects: medium, light, then heavy resistance for the medium speed, followed by the same resistance order at the slow speed, and lastly the fast speed (Top panel, Figure 1A). Each subject was asked to track a computer generated sinusoidal target consisting of five cycles as they performed a single limb squat exercise (Figure 1B). Even though the movement speeds varied across nine testing conditions, the individual's body position and the required knee angular control remained constant. Specifically, the target trajectory is always fixed across all speeds, corresponding to a range of knee motion of approximately 30 degrees of knee flexion to full knee extension. Instantaneous visual feedback of actual knee position (black sinusoidal line, Figure 1C) was provided to subjects on the same monitor as the target trace (gray sinusoidal line, Figure 1C). No further feedback, like knowledge of results, was given other than instantaneous visual feedback.

Within each testing condition, the brake resistance was programmed to be removed unexpectedly for a pre-determined time equivalent to approximately 10% of the cycle duration (200, 250, and 500 ms for 0.6, 0.4, and 0.2 Hz, respectively). The timing of brake release was randomly inserted in one cycle from 2 – 5, and always occurred during early knee flexion phase (i.e. 10 degrees of knee flexion) in order to perturb the ongoing knee flexion motion (the rectangle overlying the sinusoidal lines, Figure 1C). Before data collection, subjects performed two practice trials at the medium speed to familiarize themselves with the task apparatus.

Data Collection

At the beginning of each testing condition, subjects stood on a platform and were attached to the custom designed device with the hip and knee extended and the ankle in the neutral position [15]. The brake system was programmed to control levels of resistance throughout the entire experiment. Our pilot studies showed a strong correlation between the angular and linear displacements of the knee ($R^2 = 0.97$). A 15-cm linear displacement corresponds to 30 degrees of knee flexion during single leg squatting. The testing leg was secured by a Velcro strap around the knee to maintain a fixed position on the force sensor attached to the device for force measurements (Figure 1C). To display real-time visual feedback, a computer monitor was positioned approximately 30 cm in front of the subject and was adjusted to the subject's body height. To indicate the start of each test, a visual countdown of five seconds to target tracking was given. There were nine trials in total (3 speeds $\times$ 3 resistances), one trial per testing condition per subject. Within each trial, there were five repeated cycles. Force and knee kinematic data were synchronized and recorded at 2000 Hz using custom LabVIEW software (National Instruments; Austin, TX).

Electromyography

In a subset of 10 subjects, electromyography of the rectus femoris, vastus lateralis, vastus medialis and lateral hamstrings was collected. Surface electrodes (Ag/AgCl; 8 mm diameter; 20 mm inter-electrode distance) were placed over the muscle belly of each muscle [18, 19]. All electrodes were secured with pre-wrap to minimize movement of the electrodes during testing.

Once electrodes were securely placed, each subject was seated in the chair of a Kin-Com isokinetic dynamometer (Chattecx Corp.; Chattanooga, TN), with the knee joint positioned at 90 degrees. Subjects were then instructed to perform three maximum volitional isometric contractions in both knee flexion and knee extension. Subjects were given one-minute rest between each contraction to avoid fatigue. Verbal encouragement was given during each of the contractions. The mean of the maximum activity was then used to normalize all electromyographic data for each respective muscle. All EMG sampling during MVC and visuomotor task was performed using LabVIEW software (National Instruments; Austin, TX) and sampled at 2000 Hz.

Data Analysis

All analyses were conducted using Custom Matlab software (MathWorks, Natick, MA). In each trial, the onset of each cycle was first identified. Movement error was then quantified as the difference between target and user's signals at each time point within each cycle. Root-mean-square (RMS) of errors across all time points in each cycle was calculated to represent the average error performance for each cycle. We separated the "perturbed" cycle from the other four "non-perturbed" cycles for subsequent analyses. The EMG signal was band pass filtered from 20–2000 Hz and the RMS was calculated every 5 ms over the 50–200 ms after the perturbation. The onset was defined as the point where the brake would be released (unperturbed) or was released (perturbed). All EMG for the perturbed condition was normalized to the EMG during the unperturbed condition.

Non-perturbed cycles—To track the cycle-by-cycle improvement in single-leg squat performance, we examined the reduction of movement errors by comparing RMS errors across five consecutive cycles. To determine whether performance of a single-leg squat is velocity-dependent and/or resistance-dependent, RMS errors were averaged across all non-perturbed cycles within each individual at each velocity, at each level of resistance, and in each condition. Group means of RMS errors were first calculated by averaging across all subjects and then were compared across different velocities, different levels of resistance, and different conditions.

Perturbed cycles—To investigate the “reactive feedback control” in response to an unexpected perturbation (i.e. release of the brake resistance) during single-leg squatting, we examined perturbation-evoked changes in errors and force. We quantified rates of error and force changes by dividing absolute values of error and force changes to its corresponding perturbation time period. In order to examine perturbation effects across different conditions, we normalized rate of error and force changes to the average of absolute change of error and of force during the non-perturbed cycles in each condition. All variables then were averaged over all subjects to create group means for each condition. The change in electromyography of each muscle during the long latency period of the perturbation (50–200 ms) was calculated relative to the muscle activity of the same time of a cycle without a perturbation. Percent change was calculated by dividing the difference between the perturbed and unperturbed activity by the unperturbed activity. Activation of each muscle was normalized to the activity of the maximum volitional isometric contraction to enable averaging across subjects.

Statistical Analysis

Statistical comparisons were made using SAS/STAT software (SAS, Cary, NC, USA). A two-way mixed model ANOVA with repeated measures for velocity and resistance and a one-way mixed model ANOVA with repeated measures for cycle and condition were used to assess significant changes in errors and/or forces with/without the perturbation. Electromyography data for the quadriceps and hamstring muscles were analyzed using a two-way mixed model ANOVA with repeated measures. When the ANOVA was significant, post hoc analyses were performed using Tukey’s honest significant difference test. For models using an ANOVA, the effect size is determined by calculating the η^2 . In followup tests using Tukey Tests, the effect size was determined by calculating the Cohen’s d . The level for statistical significance was set at $P < 0.05$.

RESULTS

General Error Analysis

Individual traces of target and user signal across nine testing conditions (3 speeds $\times$ 3 resistances) are depicted in Figure 2 from a typical subject (upper panels; Figure 2A–2C). Reproducible force profiles, characterized by the smallest amplitude at the lowest resistance (5% of body weight) and the highest amplitude at the highest resistance (15% of body weight), were observed throughout the entire test. This supports that the brake resistance is precisely controlled at a pre-determined level as movement speeds were changed from 0.2

Hz to 0.6 Hz. In addition, a general trend is observed; that is, greater discrepancies between target and user signal (gray and black traces, respectively) were observed in conditions with higher speeds and/or resistances as compared to conditions with lower speeds/resistances. It is also noteworthy to mention that the perturbation triggered by the unexpected brake release has a significant impact on ongoing knee motion and force output (rectangles; Figure 2A–2C). It is clear that the user signal (black trace) was significantly deviated from the target signal (gray trace) during the perturbation period, especially in conditions with the highest resistance (Figure 2C). Accordingly, the force exerted by the subject dropped sharply during the perturbation period due to an abrupt removal of the brake resistance.

Movement Speed (Velocity) and Resistance

Similar findings were also observed in group averages of RMS errors across non-perturbed cycles (cycle 1–5) for each condition. Overall, errors increase as movement speed or resistance increases (Figure 3A). There is a clear pattern showing that healthy adults significantly improved movement accuracy after the third repetition (i.e. cycle 3). The RMS error is significantly lower in cycle 3 to cycle 5 as compared to cycle 1 (post-hoc, all P s < 0.0001, Cohen's d =2.8, 2.7, 2.8, respectively) or cycle 2 (post-hoc, P =0.02, 0.005, 0.001; d =1.1, 0.9, 1.0, respectively Figure 3B -Cycle). In addition, a progressive increase in speed resulted in a linear increase in RMS error (P <0.0001, effect size: η^2 =0.50; Figure 3B -Velocity). A progressive increase in resistance also resulted in increased error (p <0.0001, η^2 =0.01, post hoc, 15% > 10% > 5%; Figure 3B -Resistance). There was an interaction of speed and resistance (P =0.0011). The highest speed error increased at each increment in resistance (P <0.0001, η^2 =0.24), but at the slow and medium speed, the lowest resistance did not respond consistently with the medium and high resistance conditions. A hierarchical order of RMS errors was illustrated when averaging across all available cycles within each condition and across all subjects to yield the overall group means for nine conditions (3 speeds $\times$ 3 resistances; Figure 3C). There was a main effect of condition (P < 0.0001, η^2 =0.60) and post hoc analysis revealed significant differences in RMS errors based on this hierarchy (post-hoc, all P s < 0.05). The hierarchical model illustrates the amplitude of the RMS error as a linear function of velocity. It suggests that the higher the velocity, the greater RMS error produced by the individual. It appears that altering resistance has minimal effects on error performance especially at the slow velocity; while the effect of resistance on error performance becomes more prominent at the higher velocity. This again suggests that, in the absence of the perturbation, the amplitude of movement error is highly correlated with the movement speed, but minimally affected by the level of force exertion.

Unexpected Perturbation Analysis (error)

In the presence of the unexpected force perturbation, the degree of the evoked response is scaled to the level of force exertion prior to the perturbation as well as movement speed. The analysis of rates of absolute error and force changes confirmed that the perturbation-induced changes in errors and forces are both velocity- and resistance-dependent (upper panels, Figure 4A and 4B). That is, a progressive increase in either velocity or resistance would result in a linear increase in error and force changes per unit of time (main effects of velocity: P =.0014, 0.0029 η^2 =0.08, 0.057; and resistance P <.0001, 0.0011 η^2 =0.11, 0.039 respectively). Post-hoc analyses showed significant increases in rate of error and force

changes observed at fast speed (0.6 Hz) compared to slow speed (0.2 Hz) or at high resistance (15% BW) as compared to low resistance (5% BW; all P s < 0.003). We also observed a similar trend when comparing rates of error and force changes across nine conditions (3 speeds $\times$ 3 resistances; Figure 4A and 4B; lower panels). The hierarchies for perturbation-induced rate of error and force changes demonstrated similar changes due to resistance at each velocity (interaction: $P=0.056$, 0.7076 , respectively). Given a velocity or resistance, the perturbation-induced rates of error and force changes were largest at the highest resistance or the highest velocity. Therefore, in the presence of the unexpected perturbation, the degree of the reactive response necessary for regaining dynamic control is crucially determined by the movement speed and resistance applied to the knee movement (force from the brake).

Unexpected Perturbation Analysis (EMG)

The change in electromyography of each muscle during the long latency period of the perturbation (50–200 ms) was calculated relative to the muscle activity of a cycle without a perturbation. The vastus medialis, rectus femoris, and vastus lateralis all increased in muscle activity as a function of resistance (all $P < 0.05$, $\eta^2 = 0.17$, 0.24 , 0.38 respectively). The response of the quadriceps EMG at each resistance was similar as velocity increased (velocity all P s > 0.05 , all $\eta^2 < 0.03$, interaction all P s > 0.05). Due to motor equivalence across synergists of the quadriceps, all three were averaged together, demonstrating a step wise pattern increasing approximately 60% from lowest to highest resistance in the slow and medium velocities, and increasing nearly 100% from the lowest to highest resistance in the fast velocity (Figure 5B). Taken together, these findings illustrate that the quadriceps muscles exhibit a doubling of activity within 200 ms in response to an unexpected event that occurs under conditions of high velocity and high resistance. As expected, there was a reciprocal decrease in lateral hamstrings activity as compared to the knee extension muscles ($P=0.03$) but no statistical difference was observed at varied resistances ($P=0.242$) and velocities ($P=0.1887$, interaction $P=0.923$). The reduction in lateral hamstrings EMG compared to the knee extension complex EMG supports an inhibition of the knee flexors within 200 ms in order to reduce the acceleration of the limb after the perturbation (Figure 5B). This inhibition coupled with the excitation to the quadriceps creates the “optimal” force couple to negate the free fall induced by the unexpected release of the brake.

DISCUSSION

In this study, we found that a progressive increase in speed and/or resistance resulted in an increase in movement error. Likewise, during unexpected perturbations, the error was high when resistance and speed were set at the highest levels (i.e. the condition with the speed at 0.6 Hz and the resistance at 15% body weight). To our knowledge, this study is the first that provides a hierarchical framework (range of task difficulties) in order to quantify the feed-forward, feedback, and overall control of the knee during a functional weight bearing task.

Movement Speed (Velocity) and Resistance

In the absence of a random perturbation, it is clear that tracking a target at high speeds challenges the neuromuscular control system. Our findings are concordant with Fitts's law

[3, 4] in that as the difficulty of the motor task increased the movement amplitude error increased. At a given level of task difficulty, faster responses tended to produce more errors. In this case, the level of task difficulty was increased in increments of movement amplitude per unit of time (i.e. increasing speed). Increased speed equating to increased difficulty has been supported in many motor control paradigms including: line tracing [20], reciprocal motions [3], and incident-anticipation [21, 22]. The effects of resistance on motor tasks has been less definitive, where increased pen weight (resistance) increased the error of a reciprocal task [3], though resistance did not influence the error of a complex repeated motion [6]. Simply increasing the resistance, however, may not necessarily become more challenging. The average error at the fast speed was two times greater than the error at the slower speed, however, the average error at the highest resistance was only 50% greater than the error at the lowest resistance. Accordingly, velocity is a larger determinant in the difficulty of a weight-bearing visuomotor task, and creates a linear increase in difficulty (RMS error).

Unexpected Perturbation Analysis (error)

During one of the flexion phases of each condition, a perturbation was delivered by releasing the brake of the apparatus for a short period of time. Unexpected perturbations are differentially challenging to the nervous system depending on the degree of resistance and speed of the task. During the unexpected perturbation, the difference in response (rate of error and rate of force) is due to purely non-volitional feedback [23, 32, 33]. It is interesting to note that unlike error of the mixed feed-forward and feedback (unperturbed) portion, resistance and velocity have an equal weight in increasing difficulty during feedback response (perturbed portion). The error rate approximately doubles when incrementing from the slowest to fastest velocity, and from the lowest to highest resistance. Similarly, the force rate increases by approximately 70% when incrementing from slow to fast, and light to heavy resistance (Figure 4A, 4B top panel). When examining the progression of the combination of velocity and resistance, instead of a completely linear nature, there is a step-wise increase of error and force rate. The bottom panels of Figure 4A and 4B demonstrate that the least resistance (5% BW) of each velocity condition provides slightly less impact on the error and force rate than the highest resistance (15% BW) of the speed just below it.

Unexpected Perturbation Analysis (EMG)

Electromyography of the three quadriceps muscles during the long latency reflex demonstrated an increase in activity compared to the state of the unperturbed central set. At larger resistances, the muscles are increasingly elicited in a step-wise pattern that differs from the unperturbed. These findings are in support of previous literature [23–27]. Although our study suggests equivalent supra spinal influence of all three muscles, one study suggests that the rectus femoris is the only quadriceps muscle with supra spinal contributions to the long latency component [24]. The difference in findings is most likely due to the fact that our study involves a weight bearing visuomotor task compared to a seated, open chain movement. This suggests that the integration of vestibular, somatosensory, and visual feedback is an important determinant of the magnitude of the long latency reflex during upright stance.

During the lowest resistance conditions (5% BW) activity tends to be slightly increased in the lateral hamstrings. However, the same muscle group is inhibited in all other conditions (Figure 5B). This indicates that when resistance is low a slight increase in joint stiffness may be the optimal strategy to prevent further error, and indeed does provide the least error within each velocity (Figure 4A). As resistance increases, however, stiffening is no longer an optimal strategy thus the hamstrings demonstrate increasing inhibition, allowing the increasing activity of the quadriceps to slow (or reverse) the fall of the individual. Previous investigations have discussed the multi-system nature of both spinal and supra spinal inhibition during the long latency period of a perturbation [28–31]. Our study is consistent in that there is a clear trend of antagonist inhibition scaled with resistance (muscle activation) of both the agonist and antagonist during the stretch response.

The presented testing paradigm demonstrates that under each testing condition, learning occurs very rapidly (Figure 3B). This is advantageous to achieve an accurate measure of an individual's ability to perform in a short time, allowing for a potentially clinically feasible assessment. Currently in the clinic, a combination of multiple tests is necessary to predict disability, e.g. falls in the elderly [34, 35], or return to play in the ACL reconstructed athlete [36–38]. In this testing paradigm, the shortest testing condition (0.6 Hz) lasts 8.3 seconds and the longest (0.2 Hz) 25 seconds; allowing collection of all nine conditions in under 10 minutes. This novel weight bearing test provides a quantitative assessment of both feed-forward and feedback control (motor function) of the lower extremity through a range of conditions in a very short amount of time.

CONCLUSION

In this study we have presented a hierarchical framework (range of task difficulties) to assess feed-forward and feedback control during a functional weight-bearing, visuomotor task. The rapid ability to achieve intra-individual proficiency (within 3 cycles), speed of testing (each condition in under 30 seconds), and the ubiquitous nature of the partial single limb squat, provides the prospect of a framework to measure feed-forward and feedback control in people with and without gait and posture impairments.

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Highlights

- We studied feed-forward/feedback control during a novel weight bearing task
- Movement error was amplified by the velocity change during unexpected perturbations
- Long latency reflexes modulated the feedback control to postural perturbations
- Neuromuscular control problems may be captured using this novel weight bearing task
- Understanding neuromuscular control strategies help establish effective interventions

A. Study Paradigm

B. Motor task

C. Experimental setup

Figure 1. Illustrations of study paradigms (A), motor tasks (B), and experimental setup (C) Nine testing conditions (3 speeds $\times$ 3 resistance levels) were assigned to each subject in order: the medium speed in combination with three levels of resistance, the slow speed in combination with three levels of resistance, and the fast speed in combination with three levels of resistance (A). The motor task consists of five cycles of the sinusoidal waveforms (i.e. target signal) set at three pre-determined frequencies: 0.2, 0.4, and 0.6 Hz, corresponding to slow, medium, and fast movement speeds (B). The target signal corresponded to ~ 30 degrees of knee flexion and knee extension. Subjects were instructed to track computer generated sinusoidal targets as they performed a single limb squat exercise (C). Instantaneous visual feedback of actual knee position (the black trace) was provided to subjects on the same monitor as the target trace (the gray trace) (C). The brake system was turned off for a pre-determined period of time within a cycle to produce a perturbation. The rectangle overlaid on sinusoidal signals indicated the time period when the resistance was released. The bottom traces depicted force readings over time (C). BW: body weight.

Figure 2. Motor performance from a typical participant across nine testing conditions

Time series data of user's signals (black traces) overlaid with target signals (gray traces) across three speeds (slow, medium, and fast), with three levels of resistance (5%, 10%, and 15% BW) in each (Upper traces in **A–I**). The peak-to-peak amplitude of target signal corresponded to 30 degree of knee flexion to full knee extension and was consistent across all testing conditions; whereas the amplitude of force was scaled to the level of brake resistance (lower traces in **A–I**). Accordingly, the greatest force amplitudes were observed during conditions with the 15% of BW resistance (**C, F, I**). Rectangles indicate the time periods when the brake resistance was removed. Note that the break release perturbed ongoing knee motion and force production. BW: body weight.

Figure 3. Group averages of root-mean-square (RMS) of errors during non-perturbed cycles
 RMS errors were averaged over all subjects for each non-perturbed cycle within each condition (A). Recall that there were nine conditions, five cycles per condition. To determine factors that might influence movement accuracy, RMS errors were averaged across cycles, velocity, and resistance (B). In order to quantify the combination effect of velocity and resistance on movement accuracy, RMS errors were averaged across all non-perturbed cycles in each condition for each subject, and were then averaged over all subjects for statistical comparisons (C). Error bars, ± 1 SEM. BW: body weight. *: significant post-hoc differences between pairs of comparisons. †: significant post-hoc differences between the denoted condition (i.e. 0.2Hz, 5% BW) and all conditions at the medium and fast speeds. ‡: significant post-hoc differences between each denoted condition and conditions at the

medium speed with 10% and 15% BW resistance, and all conditions at fast speeds. **: significant post-hoc differences between each denoted condition and conditions at the fast speed with 10% and 15% BW resistance.

A. Rate of error changes

B. Rate of force changes

Figure 4. Group averages of rates of error and force changes across all perturbed cycles Each data point is expressed as the rate of error change (**A**) and rate of force change (**B**) during the perturbation (i.e. time period of break release). Notice that absolute changes in error and force obtained during the perturbation period were divided to its corresponding perturbation duration and expressed as rates of error or force changes. To examine perturbation effects across different conditions, we normalized rate of error and force changes to the average of absolute change of error and of force during the non-perturbed cycles in each condition (lower panels in **A** and **B**). To determine factors that might

influence movement accuracy, rate of error and force changes were averaged across velocity and resistance (upper panels in **A** and **B**). Error bars, ± 1 SEM. *: significant post-hoc differences between pairs of comparisons. †: significant post-hoc differences between the denoted condition (i.e. 0.2Hz, 5% BW) and all other conditions. ‡: significant post-hoc differences between each denoted condition and all conditions with 15% BW resistance. **: significant post-hoc differences between each denoted condition and the condition at the fast speed with 15% BW resistance. BW: body weight.

Figure 5. Percent increase of the perturbed from the non-perturbed electromyography of the agonists and antagonists

Percent change of the electromyography of the long latency period of the perturbed cycle vs the equivalent time period of the non-perturbed cycle. Three of the quadiceps muscles were measured (A) including the Vastus Medialis (black square), Vastus Lateralis (Light gray square), and the Rectus Femoris (dark gray square). Due to motor equivalence of the quadiceps, activity from all three muscles was averaged (black square) and represented with the lateral hamstrings (white square) (B). The symbol ‘*’ denotes significant differences between rectus femoris and vastus lateralis ($p < 0.05$). In panel B, symbols (*, #, &, +) represent post hoc groupings of conditions. For example, * represents that electromyography activity under combinations of speed + percent body weight resistance of: 0.2Hz + 15%, 0.4Hz + 15% BW, 0.6Hz + 10% BW, and 0.6 Hz + 15% BW are significantly different the other speed + resistance combinations ($p < .05$). There was no statistical difference between conditions of the lateral hamstrings ($p > 0.05$).