Muscle co-contraction patterns in robot-mediated force field learning to guide specific muscle group training

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Abstract

BACKGROUND: Muscle co-contraction is a strategy of increasing movement accuracy and stability employed in dealing with perturbation of movement. It is often seen in neuropathological populations. The direction of movement influences the pattern of co-contraction, but not all movements are easily achievable for populations with motor deficits. Manipulating the direction of the force instead, may be a promising rehabilitation protocol to train movement with use of a co-contraction reduction strategy. Force field learning paradigms provide a well described procedure to evoke and test muscle co-contraction.

OBJECTIVE: The aim of this study was to test the muscle co-contraction pattern in a wide range of arm muscles in different force-field directions utilising a robot-assisted force field learning paradigm of motor adaptation.

METHOD: 42 participants volunteered to participate in a study utilising robot-assisted motor adaptation paradigm with clockwise or counter-clockwise force field. Kinematics and surface electromyography (EMG) of eight arm muscles has been measured.

RESULTS: Both muscle activation and co-contraction was earlier and stronger in flexors in clockwise condition and in extensors in the counter-clockwise condition.

CONCLUSIONS: Manipulating the force field direction leads to changes in the pattern of muscle co-contraction.

Keywords: Motor adaptation, force-field learning, EMG, co-contraction, rehabilitation

1. Background

Motor adaptation is defined as learning of a previously known motor skill in the presence of an extra perturbation. It is characterized by a gradual improvement of performance, but the skill fades quickly after the perturbation is no longer in place. It is typically studied with error-based experimental paradigms, such as visuo-motor rotation and force-field tasks (Krakauer & Mazzoni, 2011). The concept of motor adaptation, alongside more complex motor learning, has been applied to model motor rehabilitation and in consequence formulate the recommendations for interventions (Dipietro et al., 2012).

1.1. Muscle co-contraction in motor adaptation

Motor adaptation is accompanied by a typical muscle activation pattern, with an initial increase of muscle activity and co-contraction followed by a reduction in both muscle activity and co-contraction thereafter (Darainy & Ostry, 2008; Thoroughman & Shadmehr, 1999). This pattern is thought to be a compensatory strategy to reduce movement variability (Osu, Morishige, Miyamoto, & Kawato, 2009; Seidler-Dobrin, He, & Stelmach, 1998) and increase the task performance accuracy (Gribble, Mullin, Cothros, & Mattar, 2003) at a lower energetic cost (Huang and Ahmed, 2013). A kinematic measure of summed error decrease is typically associated with reduction in muscle co-contraction (Huang & Ahmed, 2014; Milner & Franklin, 2005).

Co-contraction of antagonist muscles depends on movement direction (Darainy, Malfait, Gribble, Towhidkhah, & Ostry, 2004; Gomi & Osu, 1998; Perreault, Kirsch, & Crago, 2002). Darainy and Ostry (2008) demonstrated, in both dynamic and stable adaptation conditions, that the co-contraction pattern varies depending on movement direction alongside the strength of the external force. Since the co-contraction was still present even when the kinematic and EMG measures did not show any effects of learning anymore, they assumed that this process plays a central role in movement regulation by the nervous system.

1.2. Muscle co-contraction in motor deficits

Excessive muscle co-contraction is observed in movement of older adults (Darling, Cooke, & Brown, 1989; Hortobagyi et al., 2009; Schmitz, Silder, Heiderscheit, Mahoney, & Thelen, 2009; Seidler-Dobrin et al., 1998). In motor adaptation force field protocols, older adults use more muscle co-contraction than young adults, which however reduces normally as the adaptation takes place, accompanied by the reduction of metabolic cost (Huang & Ahmed, 2014).

Muscle co-contraction accompanies motor deficits in hemiplegia caused by stroke. Braendvik and Roeleveld (2012) also found increased co-contraction of the muscle antagonist to the spastic one in hemiplegic cerebral palsy children, finding however no support for the influence of that phenomenon on force control. The authors infer thus the co-contraction has a role in movement stability.

Greater muscle co-contraction is thought to be accompanied with higher metabolic cost, as seen in older adults in locomotion (Hortobagyi, Finch, Solnik, Rider, & DeVita, 2011; Mian, Thom, Ardigo, Narici, & Minetti, 2006; Ortega & Farley, 2015) and hand motor learning (Huang & Ahmed, 2014). Reducing co-contraction can thus lead to reduction in metabolic cost of movement (Huang, Kram, & Ahmed, 2012). The reduction of muscle co-contraction is postulated to reduce spasticity (Kamper & Rymer, 2001) and thus it has been a target for rehabilitative programs (Wright, Rymer, & Slutzky, 2014).

Muscle co-contraction has been tested extensively for antagonist pairs of muscles both in health and pathology. Since it is a strategy of increasing movement accuracy and stability employed in dealing with perturbation of movement, it is a valuable rehabilitation target. The direction of the movement influences the pattern of co-contraction, but not all movements are easily achievable for populations with motor deficits. Manipulating the direction of the force instead, that has already proved effective in kinematic results (Patton, Stoykov, Kovic, & Mussa-Ivaldi, 2006), may be a promising rehabilitation protocol to train movement with use of a co-contraction/co-contraction reduction strategy. Force field learning paradigms provide a well described procedure to evoke and test muscle co-contraction. The aim of this study is to test muscle co-contraction patterns in a wide range of arm muscles during a reaching task in different force-field directions utilising a robot-assisted force field learning paradigm of motor adaptation.

2. Method

2.1. Participants

Forty-two right handed healthy adults (median age: 26.5; 20-42; 8 male) volunteered to participate in the study. The data of seven participants were excluded for the following reasons: psychiatric history (1), problems during data acquisition (2), movement onset consistently too early (1), profound movement artefacts (3). They were randomized into two conditions: 17 clockwise force field and 18 counter-clockwise. The study was approved by University of East London ethics committee (UREC_1415_29) and it was conducted according to the Declaration of Helsinki.

2.2. Apparatus

A shoulder/arm robotic manipulandum (MIT-Manus, Interactive Motion Technologies, Cambridge, MA, USA) was used to generate the force field and record the kinematic data. The participants held the end-effector handle with their right hand (70º shoulder extension, 120º elbow flexion, semi-pronated arm) and their forearm was placed in a custom-made thermoplastic attached to the joystick for the support of the reaching arm against gravity. The shoulders were at the same level of the end-effector and safety belt straps were used to restrict trunk movements. A vertical screen situated at eye-level provided online feedback on the position of the handle. Kinematic parameters of each reach trial were recorded by the robotic device with sensors incorporated in the robot actuators. End-effector position and velocity (along the x and y axes), and exerted forces (along x, y and z axes; N) were sampled at 200 Hz and stored for the off-line analysis.

EMG (µV) was recorded from the right arm Anterior Deltoid (AD), Posterior Deltoid (PD), Biceps Brachii (BB), Triceps Brachii (TB), Extensor Carpi Radialis (ECR), Flexor Carpi Radialis (FCR), Brachioradialis (BR) muscles and the left arm Biceps Brachii (BBleft). Bipolar superficial electrodes with a fixed 1.5 cm inter-electrode distance were positioned on each muscle, according to SENIAM guidelines (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000). Data were sampled at 1 kHz and digitized via a 14 bit analogue-to-digital convertor (DataLog EMG system, Biometrics Ltd, Newport, UK). In order to synchronize kinematic and physiological signals, the robotic device sent a TTL pulse at each visual cue (i.e. trigger at the beginning of a trial, time = 0 s) via a BNC cable to the EMG system.

2.3.Procedure

The participants were seated in a comfortable chair in front of the robotic manipulandum. Their task was to reach out towards the north-west direction from a central starting point (1 cm diameter on the screen) to a peripheral target within 1.0 – 1.2 seconds after a visual cue (the peripheral target changing colour from white to red/orange). The arm was then repositioned to the central point by the robot after each trial (i.e. passive arm return so as not to interfere with the motor adaptation process). The motor adaptation procedure consisted of three conditions: Familiarization, Motor Adaptation and Wash Out, each comprising of 96 trials. During the Familiarization and Wash Out phase the participants operated in null field condition. During the Motor Adaptation condition the robot applied a 25 N sm^{-1} velocity-dependent force-field (clockwise or counter-clockwise, depending on the experimental condition), perpendicular to the trajectory of the joystick.

2.4. Data analysis

2.4.1. Kinematics

Offline data analyses were run in MatLab 2013b (The MathWorks, Inc.). Kinematic data from the robot were interpolated in order to match the sampling rate of the EMG signals. Reaching movements were described by a starting time point (movement onset defined by a speed profile exceeding 0.03 m s^{-1}) and by an end time point (movement offset defined by a speed profile lower than 0.03 m s^{-1}). Kinematics and kinetics trial-by-trial trajectory error was quantified, using established methods, by calculating the summed error (cm), defined as the absolute cumulative perpendicular distance (values are only positives regardless of path directionality) between the actual trajectory and the ideal straight line connecting the central starting point and the peripheral target. It consists of a measure of error for the whole duration of the reaching movement, from movement onset to movement offset and captures both changes in trajectory and movement duration that may occur during motor adaptation (Hunter, Sacco, Nitsche, & Turner, 2009; Osu, Burdet, Franklin, Milner, & Kawato, 2003). Additional measures included peak velocity (m s^{-1}) and peak x-y planar force production by the subject (N) during the reach trial.

2.4.2. EMG

Trial-by-trial raw EMG data were first de-trended, high-pass filtered at 45 Hz (Butterworth, order 3), notch filtered (50Hz) and rectified. Each muscle activity was normalized to the maximum value registered in that muscle across the whole experimental recording (i.e. activation ratio, %) in order to minimize variability across subjects due to possible variation in electrode-skin impedances. After pre-processing of the data, maximum EMG activation (Peak EMG; μV) and latency (Peak EMG latency relative to movement onset; ms) were calculated for each trial within a time period ranging from movement onset and movement offset. For each subject, trial-by-trial filtered and rectified EMG signals were used to assess muscle pair co-activation between all the possible combinations of the muscles of the right arm (i.e. 21 pairs in total) following the "wasted contraction" calculation, where the minimum shared EMG activity between the profiles of two muscles for each time point in the single trial was considered, creating a new co-contraction profile (Gribble et al., 2003; Huang & Ahmed, 2014; Thoroughman & Shadmehr, 1999). Although this type of analysis was traditionally applied to antagonist pairs of muscles, in this paper the pool of pairs is extended to include all possible combinations of co-contraction.

2.5.Statistical analysis

All measures of motor adaptation were assessed trial-by-trial for each subject and then averaged in 6 blocks of 16 trials for each condition and across subjects (N = 35). Statistical analysis of motor adaptation measures then focused on differences between 8 blocks of major interest: block 6 (Familiarization trials 81-96, null field), block 7 (Motor Adaptation trials 1-16, force field), block 8 (Motor Adaptation trials 17-32), block 9 (Motor Adaptation trials 33-48), block 10 (Motor Adaptation trials 49-64), block 11 (Motor Adaptation trials 65-80), block 12 (Motor Adaptation trials 81-96) and block 18 (Wash Out trials 81-96, null field). Statistical analyses were run through SPSS 20 (IBM) and MatLab 2013b. Averaged block data were first tested for normality with the Kolmogorov-Smirnoff test. The vast majority of data were normally distributed. Where data were not normally distributed, non-parametric tests were also used, but in all circumstances these did not yield different results to the parametric tests so are not presented here.

Each measure was analysed in a 2 (force direction: clockwise vs counter-clockwise; between subjects) x 8 (block; within subjects) ANOVA design. Post hoc paired t-tests with Bonferroni correction for multiple comparisons was applied to analyse the differences between block 6 and block I, with $i = 7,\ldots 12,18$ (7 comparison in total, $p < 0.007$).

3. Results

3.1. Kinematics

There were no significant differences in movement onset (p=0.086), movement offset (p=0.875), maximum velocity (p=0.450). There was a significant Block x Force Direction interaction effect for maximum force (F(2.734,90.213)=26.780, p<0.001). Maximum force was higher in the clockwise than counter-clockwise condition in all blocks of Motor Adaptation, whereas it was similar during Late Familiarization and Early Wash Out (F(1,33)=29.856, p<0.001). There was also a significant main effect of block (F(2.734,90.213)=186.530, p<0.001). There was a significant Block x Force Direction interaction effect for summed error (F(2.663,87.871)=4.891, p=0.005) with a main effect of block (F(2.663,87.871)=78.536, p<0.001) but not of force direction (p=0.135). Figure 3.1. presents the kinematics results, for detailed statistics see Appendix A.

3.2. Muscle activation

Figure 2 presents the muscle activation results in four representative muscles. Peak muscle activation increased in the beginning of Motor Adaptation (block 7) to decrease gradually throughout the process of adaptation both in clockwise and counter-clockwise conditions (see Appendix B for statistics summary).

Muscle activation time differed between clockwise and counter-clockwise condition in the following muscles; earlier EMG peak latency in clockwise in: BB (F(1,33)=9.904, p=0.003), FCR (F(1,33)=31.288, p=0.001); earlier EMG peak latency in counter-clockwise: PD (F(1,33)=35.522, p=0.000), TB (F(1,33)=27.274, p=0.000), ECR (F(1,33)=48.081, p=0.000), BR (F(1,33)=5.655, p=0.023).

Peak EMG activation differed between clockwise and counter-clockwise condition in the following muscles: higher in clockwise: FCR (F(1,33)=6.789, p=0.014), and higher in counter-clockwise: TB (F(1,33)=14.322, p=0.001), ECR (F(1,33)=12.295, p=0.001).

There was a significant Block x Force Direction interaction effect in the peak EMG activation for the following muscles: BB (F(3.129,103.252)=2.946, p=0.034), ECR (F(2.824,93.176)=5.631, p=0.002), FCR (F(3.206,105.793)=4.361, p=0.005).

3.3.Muscle co-contraction

Significant pairs of muscles are presented in Figure 3. The peak muscle co-contraction increased in the beginning of Motor Adaptation (block 7) and decreased gradually throughout the process of adaptation (see Table 3 in Appendix C for statistics summary).

Muscle co-contraction time differed between clockwise and counter-clockwise condition; earlier co-contraction peak latency was observed in clockwise in: AD-FCR (F(1,33)=6.692, p=0.014), BB-FCR (F(1,33)=16.746, p=0.000), earlier co-contraction peak latency in counter-clockwise: AD-PD (F(1,33)=6.409, p=0.016), PD-BB (F(1,33)=13.893, p=0.001), PD-TB (F(1,33)=14.322, p=0.001), PD-ECR (F(1,33)=64.285, p=0.000), PD-BR (F(1,33)=32.959, p=0.000), BB-ECR (F(1,33)=6.477, p=0.016), TB-ECR (F(1,33)=86.724, p=0.000), TB-BR (F(1,33)=22.871, p=0.000), ECR-BR (F(1,33)=23.419, p=0.000).

Peak co-contraction was higher in the counter-clockwise than clockwise condition only in the following pairs of muscles: PD-TB (F(1,33)=4.276, p=0.047), PD-ECR (F(1,33)=10.954, p=0.002), BB-TB (F(1,33)=9.058, p=0.005), BB-ECR (F(1,33)=7.674, p=0.009), TB-ECR (F(1,33)=19.921, p=0.000), TB-BR (F(1,33)=12.843, p=0.001), ECR-BR (F(1,33)=11.934, p=0.002).

There was a significant Block x Force Direction interaction effect in the peak co-contraction for the following pairs of muscles: AD-FCR (F(2.642,87.182)=3.825, p=0.016), AD-BR (F(2.577,85.033)=3.181, p=0.035), PD-ECR (F(3.377,111.438)=3.148, p=0.023), BB-FCR (F(3.652,120.518)=4.297, p=0.004), TB-ECR (F(3.294,108.710)=8.617, p<0.001), ECR-BR (F(2.968,97.944)=2.974, p=0.036), FCR-BR (F(3.757,123.980)=2.627, p=0.041).

4. Discussion

Muscle activation and co-contraction increased in the beginning of the motor adaptation process and gradually reduced as the motor adaptation progressed regardless of the direction of the force.

There was a pattern for the muscle activation to be earlier in the clockwise force condition in flexors (BB, FCR) and earlier in the counter-clockwise condition in extensors (PD, TB, ECR, although the flexor BR, responsible for stabilizing the elbow, was also activated earlier in the counter-clockwise condition). This force-field-specific flexor versus extensor activation pattern was also observed in peak EMG albeit in a smaller set of muscles.

Moreover, the muscle co-contraction pattern differed between the force direction conditions: pairs including the FCR, responsible for flexing movement, were co-contracted earlier in the clockwise condition, whereas pairs always including one of the extensor muscles (PD, TB or ECR) were co-contracted earlier in the counter-clockwise condition. When peak co-contraction was analysed, there were no pairs of muscles co-contracted stronger in the clockwise condition, whereas muscle pairs always including the extensor PD, TB or ECR were stronger co-contracted in the counter-clockwise condition.

4.1. Force field direction shapes co-contraction pattern

The results suggest that both the muscle activation and co-contraction pattern can be shaped by a variable as simple as the direction of the force field during robot-assisted reaching movement. For the right hand, flexors seem more active to oppose the clockwise force, and the extensors more active to oppose the counter-clockwise force field.

4.2.More activation in the counter-clockwise condition

Earlier and stronger muscle activation and co-contraction was seen in the counter-clockwise as compared to the clockwise condition. Opposing the counter-clockwise force with the right hand requires more extensor employment, whereas opposing the clockwise force employs the flexors more. It has been hypothesised that adaptive changes in muscles can be driven by different neural pathways for flexors and extensors (Hunter et al., 2009). This hypothesis seems supported by the fact that TMS stimulation over the primary motor cortex has been found to produce greater excitatory postsynaptic potentials in the BB than TB (Palmer & Ashby, 1992) which suggest that the BB is innervated to a greater extent than the TB by monosynaptic connections. If BB indeed has stronger corticospinal input, it would be reasonable to hypothesize that flexing this muscle would be easier to perform compared to the antagonist muscle, especially while a central process – motor adaptation – takes place. It can be hypothesized that as the flexing movement seems easier to elicit, it will also require less activation of the muscles in the initial contact with a novel perturbation.

4.3.Co-contraction of not only antagonist pairs

While classical co-contraction studies focus on antagonist muscle pairs to analyse the effect of motor adaptation (Huang & Ahmed, 2014; Thoroughman & Shadmehr, 1999), the results presented here suggest that the muscle co-contraction pattern is more wide-spread, showing co-contraction of muscles not only in the antagonist pairs, but even more within a flexing/extending functional muscle unit. It seems thus that the flexing versus extending functional units play a significant role in motor adaptation alongside simple joint stiffness units. Antagonist pairs of muscles showed a significant co-contraction in this study (AD-PD and TB-BB and TB-BR in the counter-clockwise condition). It seems, however, that this can be a part of a more general co-contraction pattern process, all orchestrated to produce a functional movement adapting to that of the robot-induced force field. The robust co-contraction of many muscles grows rapidly in the beginning of motor adaptation and seems to decrease to a fine-tuned pattern to produce the most effective movement as the adaptation progresses. It is accompanied by, but not limited to, stiffening the joints.

4.4.Motor adaptation – interplay between joint stiffness and opposing the force

Pronounced muscle co-contraction in the beginning of motor adaptation, reducing as the adaptation process progresses, is a known result in motor adaptation paradigms in different populations (Huang & Ahmed, 2014; Thoroughman & Shadmehr, 1999). Similarly, muscle synergies utilised during motor adaptation have certain dynamics, with modules responsible for joint stiffness employed early in the process, followed by more fine-tuned modules that directly oppose the perturbation utilized in force field paradigms (Oscari, Finetto, Kautz, & Rosati, 2016). Enhancing the muscle stiffness in the first phase of motor adaptation is not the most efficient way to deal with perturbation, since it increases the metabolic cost, but is still a valuable strategy to reduce kinematic error (Huang & Ahmed, 2014; Oscari et al., 2016).

4.5.Neuropathology

Muscle co-contraction is often viewed as a sign of pathology in the motor system. For example, in stroke population, muscle co-contraction of antagonist pairs is viewed as an expression of pathologic stiffness of the joint (Hammond et al., 1988). Muscle co-contraction is also present in stroke within flexor (AD-BB) and extensor (PD-TB) synergies which leads to pathological stereotypical movements (Wright et al., 2014). The contribution of these pathological co-contractions to the level of impairment is still under discussion (Busse, Wiles, & van Deursen, 2006; Chae, Yang, Park, & Labatia, 2002; Gowland, deBruin, Basmajian, Plews, & Burcea, 1992).

Also muscle synergies have been found altered in the stroke population. Cheung (Cheung et al., 2012) has outlined three possible strategies of change in muscle synergies after stroke. In mild to moderate impairment, the healthy modules seem to be preserved, even though the muscle activation of the affected and unaffected arm appear different. In severe impairment, the modules are merged, producing a characteristic co-contraction – or co-activation – activity pattern. A third mechanism, not connected to the impairment severity but to the time after stroke, was fractionation of the modules, explaining the EMG response with a greater number of muscle synergies in the healthy arm. This effect is hypothesised to be an adaptive mechanism to compensate for the difficulties in movement. Changes and merging of muscle synergies in stroke have also been reported in other studies (Clark, Ting, Zajac, Neptune, & Kautz, 2010; Gizzi, Nielsen, Felici, Ivanenko, & Farina, 2011; Roh, Rymer, Perreault, Yoo, & Beer, 2013).

4.6.Clinical implications

Targeting the normalization of muscle co-contraction patterns or muscle synergies seems a valuable rehabilitation target. Wright and colleagues (2014) have shown that muscle coupling – both healthy and pathological – can be decoupled using a relatively simple neurofeedback protocol. Hence, for rehabilitative purposes, muscle pair co-contraction analysis seems valuable, since it provides a framework in EMG-based feedback patterns easy to follow for the patient. Relying on simpler indicators of activity – muscle co-contraction instead of muscle synergies – can facilitate the process of translating the findings into neurorehabilitative interventions.

It remains to be established how an intervention to change the muscle co-contraction in an impaired population would affect the hand function per se. This question warrants further research including neuropathological populations to eventually establish a recommended strategy for individual patients. Based on Cheung and colleagues' (2012) observations, some patients may require assistance in merging fractionated modules, whereas other patients may require the contrary - decoupling of merged modules. Robot-assisted motor adaptation protocols are robust in eliciting muscle co-contraction and co-contraction reduction patterns, which can be a great starting point to assess the status of the muscle co-contraction/modularization. Hence, with use of motor adaptation protocols, relevant individualised therapeutic targets can be established and the design of precise therapeutic programs can be further facilitated, modifying the direction of movement or force field to induce specific co-contraction patterns synergies.

Declaration of Interest

The authors declare no conflict of interest.

References:

Braendvik, S. M., & Roeleveld, K. (2012). The role of co-activation in strength and force modulation in the elbow of children with unilateral cerebral palsy. *J Electromyogr Kinesiol, 22*(1), 137-144. doi: 10.1016/j.jelekin.2011.10.002

Busse, M. E., Wiles, C. M., & van Deursen, R. W. (2006). Co-activation: its association with weakness and specific neurological pathology. *J Neuroeng Rehabil, 3*, 26. doi: 10.1186/1743-0003-3-26

Chae, J., Yang, G., Park, B. K., & Labatia, I. (2002). Muscle weakness and cocontraction in upper limb hemiparesis: relationship to motor impairment and physical disability. *Neurorehabil Neural Repair, 16*(3), 241-248.

Cheung, V. C., Turolla, A., Agostini, M., Silvoni, S., Bennis, C., Kasi, P., . . . Bizzi, E. (2012). Muscle synergy patterns as physiological markers of motor cortical damage. *Proc Natl Acad Sci U S A, 109*(36), 14652-14656. doi: 10.1073/pnas.1212056109

Clark, D. J., Ting, L. H., Zajac, F. E., Neptune, R. R., & Kautz, S. A. (2010). Merging of healthy motor modules predicts reduced locomotor performance and muscle coordination complexity post-stroke. *J Neurophysiol, 103*(2), 844-857. doi: 10.1152/jn.00825.2009

Darainy, M., Malfait, N., Gribble, P. L., Towhidkhah, F., & Ostry, D. J. (2004). Learning to control arm stiffness under static conditions. *J Neurophysiol, 92*(6), 3344-3350. doi: 10.1152/jn.00596.2004

Darainy, M., & Ostry, D. J. (2008). Muscle cocontraction following dynamics learning. *Exp Brain Res, 190*(2), 153-163. doi: 10.1007/s00221-008-1457-y

Darling, W. G., Cooke, J. D., & Brown, S. H. (1989). Control of simple arm movements in elderly humans. *Neurobiol Aging, 10*(2), 149-157.

Dipietro, L., Krebs, H. I., Volpe, B. T., Stein, J., Bever, C., Mernoff, S. T., . . . Hogan, N. (2012). Learning, not adaptation, characterizes stroke motor recovery: evidence from kinematic changes induced by robot-assisted therapy in trained and untrained task in the same workspace. *IEEE Trans Neural Syst Rehabil Eng, 20*(1), 48-57. doi: 10.1109/tnsre.2011.2175008

Gizzi, L., Nielsen, J. F., Felici, F., Ivanenko, Y. P., & Farina, D. (2011). Impulses of activation but not motor modules are preserved in the locomotion of subacute stroke patients. *J Neurophysiol, 106*(1), 202-210. doi: 10.1152/jn.00727.2010

Gomi, H., & Osu, R. (1998). Task-dependent viscoelasticity of human multijoint arm and its spatial characteristics for interaction with environments. *J Neurosci, 18*(21), 8965-8978.

Gowland, C., deBruin, H., Basmajian, J. V., Plews, N., & Burcea, I. (1992). Agonist and antagonist activity during voluntary upper-limb movement in patients with stroke. *Phys Ther, 72*(9), 624-633.

Gribble, P. L., Mullin, L. I., Cothros, N., & Mattar, A. (2003). Role of cocontraction in arm movement accuracy. *J Neurophysiol, 89*(5), 2396-2405. doi: 10.1152/jn.01020.2002

Hammond, M. C., Fitts, S. S., Kraft, G. H., Nutter, P. B., Trotter, M. J., & Robinson, L. M. (1988). Co-contraction in the hemiparetic forearm: quantitative EMG evaluation. *Arch Phys Med Rehabil, 69*(5), 348-351.

Hermens, H. J., Freriks, B., Disselhorst-Klug, C., & Rau, G. (2000). Development of recommendations for SEMG sensors and sensor placement procedures. *J Electromyogr Kinesiol, 10*(5), 361-374.

Hortobagyi, T., Finch, A., Solnik, S., Rider, P., & DeVita, P. (2011). Association between muscle activation and metabolic cost of walking in young and old adults. *J Gerontol A Biol Sci Med Sci, 66*(5), 541-547. doi: 10.1093/gerona/glr008

Hortobagyi, T., Solnik, S., Gruber, A., Rider, P., Steinweg, K., Helseth, J., & DeVita, P. (2009). Interaction between age and gait velocity in the amplitude and timing of antagonist muscle coactivation. *Gait Posture, 29*(4), 558-564. doi: 10.1016/j.gaitpost.2008.12.007

Huang, H. J., & Ahmed, A. A. (2014). Older adults learn less, but still reduce metabolic cost, during motor adaptation. *J Neurophysiol, 111*(1), 135-144. doi: 10.1152/jn.00401.2013

Huang, H. J., Kram, R., & Ahmed, A. A. (2012). Reduction of metabolic cost during motor learning of arm reaching dynamics. *J Neurosci, 32*(6), 2182-2190. doi: 10.1523/JNEUROSCI.4003-11.2012

Hunter, T., Sacco, P., Nitsche, M. A., & Turner, D. L. (2009). Modulation of internal model formation during force field-induced motor learning by anodal transcranial direct current stimulation of primary motor cortex. *J Physiol, 587*(Pt 12), 2949-2961. doi: 10.1113/jphysiol.2009.169284

Kamper, D. G., & Rymer, W. Z. (2001). Impairment of voluntary control of finger motion following stroke: role of inappropriate muscle coactivation. *Muscle Nerve, 24*(5), 673-681.

Mian, O. S., Thom, J. M., Ardigo, L. P., Narici, M. V., & Minetti, A. E. (2006). Metabolic cost, mechanical work, and efficiency during walking in young and older men. *Acta Physiol (Oxf), 186*(2), 127-139. doi: 10.1111/j.1748-1716.2006.01522.x

Milner, T. E., & Franklin, D. W. (2005). Impedance control and internal model use during the initial stage of adaptation to novel dynamics in humans. *J Physiol, 567*(Pt 2), 651-664. doi: 10.1113/jphysiol.2005.090449

Ortega, J. D., & Farley, C. T. (2015). Effects of aging on mechanical efficiency and muscle activation during level and uphill walking. *J Electromyogr Kinesiol, 25*(1), 193-198. doi: 10.1016/j.jelekin.2014.09.003

Oscari, F., Finetto, C., Kautz, S. A., & Rosati, G. (2016). Changes in muscle coordination patterns induced by exposure to a viscous force field. *J Neuroeng Rehabil, 13*(1), 58. doi: 10.1186/s12984-016-0164-3

Osu, R., Burdet, E., Franklin, D. W., Milner, T. E., & Kawato, M. (2003). Different mechanisms involved in adaptation to stable and unstable dynamics. *J Neurophysiol, 90*(5), 3255-3269. doi: 10.1152/jn.00073.2003

Osu, R., Morishige, K., Miyamoto, H., & Kawato, M. (2009). Feedforward impedance control efficiently reduce motor variability. *Neurosci Res, 65*(1), 6-10. doi: 10.1016/j.neures.2009.05.012

Palmer, E., & Ashby, P. (1992). Corticospinal projections to upper limb motoneurones in humans. *J Physiol, 448*, 397-412.

Patton, J. L., Stoykov, M. E., Kovic, M., & Mussa-Ivaldi, F. A. (2006). Evaluation of robotic training forces that either enhance or reduce error in chronic hemiparetic stroke survivors. *Exp Brain Res, 168*(3), 368-383. doi: 10.1007/s00221-005-0097-8

Perreault, E. J., Kirsch, R. F., & Crago, P. E. (2002). Voluntary control of static endpoint stiffness during force regulation tasks. *J Neurophysiol, 87*(6), 2808-2816.

Roh, J., Rymer, W. Z., Perreault, E. J., Yoo, S. B., & Beer, R. F. (2013). Alterations in upper limb muscle synergy structure in chronic stroke survivors. *J Neurophysiol, 109*(3), 768-781. doi: 10.1152/jn.00670.2012

Schmitz, A., Silder, A., Heiderscheit, B., Mahoney, J., & Thelen, D. G. (2009). Differences in lower-extremity muscular activation during walking between healthy older and young adults. *J Electromyogr Kinesiol, 19*(6), 1085-1091. doi: 10.1016/j.jelekin.2008.10.008

Seidler-Dobrin, R. D., He, J., & Stelmach, G. E. (1998). Coactivation to reduce variability in the elderly. *Motor Control, 2*(4), 314-330.

Thoroughman, K. A., & Shadmehr, R. (1999). Electromyographic correlates of learning an internal model of reaching movements. *J Neurosci, 19*(19), 8573-8588.

Wright, Z. A., Rymer, W. Z., & Slutzky, M. W. (2014). Reducing Abnormal Muscle Coactivation After Stroke Using a Myoelectric-Computer Interface: A Pilot Study. *Neurorehabil Neural Repair, 28*(5), 443-451. doi: 10.1177/1545968313517751

APPENDIX A

Descriptive Statistics, Main effects, and Interaction Effects (Block*Group) for Kinematics

Kinematics	Null field Mean[SD]	Null field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Test of within-subjects Effects:					Test of between subjects effects:		
									Block:			Block*Condition:		Condition: CW and CCW		
	Block 6 (B6)	Block 7 (B7)	Block 8 (B8)	Block 9 (B9)	Block 10 (B10)	Block 11 (B11)	Block 12 (B12)	Block 18 (B18)	*df* (Error)	F	sig	F	sig	*df* (Error)	f	sig
Movement onset									4.289(141.546)	12.498	.000	.461	.777	1(33)	3.125	.086
CW	349.96[66.85]	326.99[54.24]	340.10[62.90]	334.94[67.44]	338.16[56.78]	341.01[61.09]	347.32[55.16]	358.34[75.76]								
CCW	325.15[32.16]	296.02[27.04]	310.97[25.67]	312.06[31.15]	316.77[30.77]	309.00[25.31]	317.89[23.52]	331.73[23.66]								
Movement offset									3.742(123.499)	10.381	.000	1.672	.165	1(33)	.033	.857
CW	1203.26[45.09]	1284.77[118.90]	1262.81[68.77]	1259.67[51.74]	1248.53[62.70]	1252.62[50.74]	1250.73[45.27]	1236.60[49.17]								
CCW	1218.66[28.17]	1328.75[88.14]	1266.74[76.96]	1245.30[50.19]	1241.47[56.32]	1239.37[36.07]	1224.91[45.37]	1215.65[49.43]								
Maximum velocity									4.205(138.778)	18.157	.000	1.288	.277	1(33)	.585	.450
CW	0.27[0.04]	0.30[0.06]	0.32[0.07]	0.32[0.06]	0.31[0.06]	0.31[0.07]	0.30[0.06]	0.26[0.04]								
CCW	0.25[0.02]	0.30[0.06]	0.30[0.06]	0.30[0.06]	0.30[0.06]	0.29[0.05]	0.29[0.06]	0.26[0.06]								
Maximum force:		*	*	*	*	*	*		2.734(90.213)	186.530	.000	26.780	.000	1(33)	29.859	.000
CW	4.28[0.54]	9.96[1.82]	10.11[1.72]	9.85[1.57]	9.79[1.71]	9.75[1.69]	9.73[1.60]	4.23[0.64]								
CCW	4.36[0.66]	7.39[1.73]	7.08[1.34]	6.83[1.27]	6.88[1.51]	6.79[1.19]	6.85[1.32]	4.52[0.81]								
Summed error:									2.663(87.871)	78.536	.000	4.891	.005	1(33)	2.353	.135
CW	2.07[0.83]	9.57[2.45]	8.72[4.10]	7.03[3.97]	6.68[4.39]	5.67[3.75]	5.22[3.24]	2.35[1.22]								
CWW	1.91[0.53]	14.87[5.70]	9.94[4.13]	8.33[3.94]	7.64[3.98]	7.15[3.43]	6.67[3.08]	2.27[2.44]								

APPENDIX B

Descriptive Statistics, Main effects, and Interaction Effects (Block*Group) for Peak EMG

Muscle and Direction (CW and CCW)	Null field Mean[SD] Block 6 (B6)	Null field Mean[SD] Block 7 (B7)	Force field Mean[SD] Block 8 (B8)	Force field Mean[SD] Block 9 (B9)	Force field Mean[SD] Block 10 (B10)	Force field Mean[SD] Block 11 (B11)	Force field Mean[SD] Block 12 (B12)	Force field Mean[SD] Block 18 (B18)	Test of within-subjects effects:					Test of between subjects effects:		
									Block:			Block*Condition:		Condition - CW and CCW:		
									df (Error)	F	sig	F	sig	*df* (Error)	F	sig
AD:									2.665(87.951)	5.398	.003	1.923	.138	1(33)	4.119	.051
CW	0.46[0.21]	0.43[0.18]	0.41[0.18]	0.410.19]	0.40[0.18]	0.41[0.19]	0.41[0.19]	0.41[0.18]								
CCW	0.45[0.15]	0.33[0.17]	0.28[0.15]	0.27[0.16]	0.29[0.17]	0.29[0.15]	0.27[0.13]	0.36[0.17]								
PD:									3.122(103.040)	53.680	.000	2.466	.064	1(33)	1.598	.215
CW	0.20[0.16]	0.49[0.18]	0.40[0.17]	0.29[0.17]	0.27[0.18]	0.26[0.17]	0.23[0.18]	0.15[0.13]								
CCW	0.17[0.06]	0.53[0.12]	0.42[0.18]	0.39[0.16]	0.36[0.16]	0.35[0.17]	0.33[0.15]	0.17[0.09]								
BB:									3.129(103.252)	39.444	.000	2.946	.034	1(33)	1.227	.276
CW	0.22[0.11]	0.49[0.19]	0.46[0.20]	0.44[0.19]	0.43[0.18]	0.43[0.19]	0.45[0.18]	0.20[0.12]								
CCW	0.23[0.07]	0.50[0.11]	0.41[0.10]	0.36[0.12]	0.36[0.12]	0.36[0.11]	0.32[0.11]	0.23[0.13]								
TB:		*		*	*	*	*		3.224(106.398)	20.200	.000	1.187	.319	1(33)	14.322	.001*
CW	0.29[0.17]	0.43[0.15]	0.35[0.14]	0.28[0.14]	0.27[0.14]	0.27[0.14]	0.26[0.14]	0.22[0.12]								
CCW	0.40[0.12]	0.58[0.13]	0.48[0.16]	0.47[0.15]	0.46[0.15]	0.45[0.14]	0.44[0.15]	0.33[0.19]								
ECR:		*	*	*	*	*	*		2.824(93.176)	51.738	.000	5.631	.002	1(33)	12.295	.001*
CW	0.16[0.11]	0.40[0.15]	0.32[0.16]	0.27[0.13]	0.25[0.15]	0.23[0.14]	0.21[0.16]	0.15[0.12]								
CWW	0.21[0.14]	0.60[0.16]	0.49[0.18]	0.45[0.16]	0.44[0.16]	0.42[0.16]	0.40[0.16]	0.17[0.15]								
FCR:					*	*	*		3.206(105.793)	42.763	.000	4.361	.005	1(33)	6.789	.014*
CW	0.18[0.13]	0.54[0.15]	0.49[0.18]	0.44[0.15]	0.42[0.14]	0.42[0.15]	0.41[0.15]	0.16[0.09]								
CCW	0.23[0.17]	0.47[0.14]	0.36[0.13]	0.31[0.14]	0.29[0.11]	0.28[0.10]	0.28[0.12]	0.15[0.11]								
BR:									2.807(92.641)	44.034	.000	1.442	2.37	1(33)	.480	.493
CW	0.17[0.10]	0.45[0.13]	0.38[0.16]	0.35[0.16]	0.34[0.15]	0.32[0.14]	0.33[0.16]	0.12[0.08]								
CCW	0.22[0.10]	0.49[0.13]	0.38[0.13]	0.34[0.11]	0.35[0.13]	0.34[0.13]	0.32[0.13]	0.21[0.15]								
Bb left:									2.533(83.575)	5.326	.004	1.291	.283	1(33)	1.702	.201
CW	0.09[0.06]	0.15[0.10]	0.16[0.12]	0.14[0.11]	0.12[0.11]	0.12[0.11]	0.14[0.14]	0.07[0.04]								
CCW	0.08[0.03]	0.14[0.19]	0.10[0.07]	0.09[0.05]	0.09[0.05]	0.08[0.05]	0.08[0.05]	0.08[0.04]								

APPENDIX C

Descriptive Statistics, Main effects, and Interaction Effects (Block*Group) for Peak Co-contraction

Muscle pairs and Direction (CW and CCW)	Null field Mean[SD]	Null field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Force field Mean[SD]	Test of within-subjects effects:					Test of between subjects effects:		
									Block:			Block*Condition:		Condition - CW and CCW:		
	Block 6 (B6)	Block 7 (B7)	Block 8 (B8)	Block 9 (B9)	Block 10 (B10)	Block 11 (B11)	Block 12 (B12)	Block 18 (B18)	*df* (Error)	F	sig	F	sig	*df*	F	sig
AD-PD:									2.453(80.935)	7.370	.001	.281	.799	1(33)	.509	.481
CW	4.44[2.86]	5.46[3.21]	4.70[3.31]	4.28[3.18]	4.00[3.10]	4.24[3.17]	3.85[3.58]	3.18[2.29]								
CCW	4.76[1.49]	6.47[2.66]	4.92[2.13]	4.60[2.16]	4.43[1.74]	4.78[1.82]	4.56[2.23]	3.90[1.90]								
AD-BB:									2.956(97.562)	5.237	.002	1.665	.182	1(33)	.509	.364
CW	5.12[2.68]	7.31[4.14]	6.47[3.01]	6.70[3.15]	6.35[3.03]	6.45[2.91]	6.42[3.36]	4.26[2.05]								
CCW	5.54[1.27]	6.84[2.60]	5.53[2.18]	5.13[2.35]	5.55[2.40]	5.53[1.92]	4.92[1.67]	4.85[2.21]								
AD-TB:									3.253(107.340)	5.489	.001	1.287	.282	1(33)	.314	.364
CW	5.38[3.29]	5.94[3.57]	5.25[2.88]	5.06[2.96]	4.70[2.70]	4.56[2.57]	4.59[3.36]	4.09[1.94]								
CC	7.40[2.09]	7.12[2.99]	5.55[2.24]	5.28[2.41]	5.45[2.14]	5.94[2.40]	5.55[1.99]	5.63[2.63]								
AD-ECR:									2.650(87.464)	15.395	.000	.461	.687	1(33)	1.313	.260
CW	3.10[1.65]	6.00[3.73]	4.89[2.98]	4.22[2.55]	4.17[2.77]	3.99[3.06]	3.81[3.67]	2.65[1.03]								
CCW	4.17[1.69]	6.93[3.39]	5.19[2.32]	5.08[2.91]	5.16[2.76]	5.13[2.26]	4.98[2.27]	2.86[1.22]								
AD-FCR:									2.642(87.182)	14.070	.000	3.825	.016	1(33)	3.120	.087
CW	3.34[2.16]	6.68[3.43]	6.03[2.80]	5.72[2.70]	5.77[3.11]	5.49[2.49]	5.70[3.18]	2.81[1.49]								
CCW	4.12[1.72]	5.67[2.10]	4.46[1.81]	3.87[1.66]	4.08[1.87]	4.16[1.51]	3.75[1.53]	3.05[1.43]								
AD-BR:									2.577(85.033)	12.041	.000	3.181	.035	1(33)	.103	.751
CW	3.36[2.00]	6.35[3.45]	5.50[2.88]	5.15[2.76]	5.32[2.69]	4.94[3.07]	5.39[3.60]	2.45[1.02]								
CCW	4.87[1.30]	6.33[2.54]	4.98[2.04]	4.70[1.85]	5.06[2.10]	5.28[2.34]	4.80[1.91]	4.16[2.16]								
AD- Bb left:									2.745(90.596)	5.432	.002	4.088	.011	1(33)	3.40	.074
CW	2.48[1.39]	4.02[2.91]	3.93[2.55]	3.51[2.62]	3.10[2.41]	3.05[2.54]	3.30[3.13]	1.94[0.52]								
CCW	2.39[0.73]	2.84[1.68]	2.13[0.79]	1.99[0.74]	2.02[0.72]	2.02[0.81]	2.08[0.93]	2.22[0.88]								
PD-BB:									2.794(7.792)	25.127	.000	1.042	.374	1(33)	2.848	.101
CW	3.76[2.27]	7.51[5.17]	5.80[4.21]	4.57[2.78]	4.05[2.40]	4.23[2.63]	3.75[2.68]	2.57[1.51]								
CCW	3.90[1.17]	8.56[2.40]	6.52[2.11]	5.96[2.45]	6.03[2.15]	5.98[2.39]	5.44[2.71]	3.62[1.75]								

PD-TB:									3.371(111.230)	38.409	.000	1.082	.364	1(33)	4.276	.047
CW	4.22[2.61]	9.60[4.22]	6.97[2.87]	5.45[3.13]	5.00[2.97]	4.95[3.14]	4.17[3.33]	2.68[1.34]								
CCW	4.80[1.57]	10.45[2.25]	8.00[2.82]	7.58[3.39]	6.88[2.41]	6.79[2.62]	6.64[3.05]	4.29[2.40]								
PD-ECR:				*	*	*			3.377(111.438)	51.645	.000	3.148	.023	1(33)	10.954	.002
CW	2.60[1.44]	7.40[3.64]	5.31[2.73]	4.06[2.54]	3.57[2.46]	3.34[2.58]	2.96[2.97]	1.97[1.01]								
CCW	3.04[1.28]	9.89[2.37]	7.67[2.74]	6.60[2.48]	6.18[2.29]	6.45[2.71]	5.75[2.77]	2.68[1.79]								
PD-FCR:									3.012(472.935)	45.502	.000	.747	.527	1(33)	.193	.663
CW	3.16[2.32]	7.48[3.76]	5.84[3.31]	4.25[2.80]	4.00[2.56]	3.92[2.85]	3.51[3.00]	1.96[1.20]								
CCW	2.96[1.04]	7.81[1.74]	5.32[1.97]	4.61[1.77]	4.42[1.47]	4.52[1.71]	4.03[1.41]	2.62[1.20]								
PD-BR:									2.845(93.898)	48.811	.000	1.051	.371	1(33)	.3.818	.059
CW	3.01[2.12]	7.85[3.78]	5.82[3.75]	4.40[2.87]	4.09[2.68]	3.71[2.70]	3.41[3.27]	1.80[0.87]								
CCW	3.62[0.94]	8.61[2.05]	6.76[2.50]	5.99[2.27]	5.83[2.04]	5.56[2.01]	5.29[2.15]	3.35[1.87]								
PD-Bb left:									2.427(80.095)	10.366	.000	3.253	.035	1(33)	1.062	.310
CW	2.28[1.89]	4.02[2.74]	3.87[3.53]	3.00[2.43]	2.57[2.28]	2.64[2.85]	2.60[2.77]	1.44[0.52]								
CCW	2.05[0.62]	3.08[1.50]	2.30[0.97]	2.16[0.66]	2.15[0.77]	2.05[0.91]	2.08[0.95]	2.05[0.88]								
BB-TB:					*	*			3.287(108.480)	19.341	.000	.853	.477	1(33)	9.058	.005
CW	4.62[2.24]	7.75[3.71]	6.13[2.93]	5.60[3.00]	4.98[2.48]	4.83[2.28]	4.94[2.82]	3.77[1.85]								
CCW	6.04[1.49]	10.1[2.28]	7.77[2.14]	7.32[2.52]	7.62[2.55]	7.75[2.93]	7.19[2.67]	5.61[2.87]								
BB-ECR:									2.834(93.534)	47.001	.000	1.717	.172	1(33)	7.674	.009
CW	2.79[1.46]	7.12[4.22]	5.71[2.76]	4.75[2.36]	4.57[2.84]	4.16[2.61]	4.00[3.12]	2.35[0.72]								
CCW	3.57[1.49]	10.0[2.65]	7.65[2.57]	6.58[2.34]	6.65[1.70]	6.15[1.81]	6.13[2.47]	3.15[1.94]								
BB-FCR:									3.652(120.518)	43.019	.000	4.297	.004	1(33)	3.374	.075
CW	3.11[2.04]	9.11[4.14]	7.97[3.37]	7.45[3.36]	6.74[2.78]	6.62[2.61]	6.50[2.81]	2.52[1.37]								
CCW	3.83[1.48]	8.50[1.93]	6.04[1.52]	5.03[1.60]	5.30[1.38]	4.91[1.24]	4.81[1.64]	3.18[1.61]								
BB-BR;									3.441(113.569)	37.493	.000	1.415	.239	1(33)	.380	.542
CW	3.31[2.24]	8.66[4.42]	7.54[3.81]	6.68[3.75]	6.30[3.71]	5.74[2.73]	6.25[3.62]	2.41[1.19]								
CCW	4.48[1.16]	9.51[2.46]	7.11[2.14]	6.62[2.48]	6.69[2.34]	6.50[2.24]	5.82[2.39]	3.90[1.97]								
BB-Bb left:									2.824(93.178)	8.168	.000	3.938	.012	1(33)	2.729	.108
CW	2.59[1.98]	4.62[3.23]	4.77[3.96]	4.14[3.42]	3.44[2.92]	3.29[2.73]	3.61[3.69]	1.86[0.38]								
CCW	2.31[0.66]	3.27[1.78]	2.69[1.13]	2.39[0.72]	2.40[0.77]	2.24[0.78]	2.22[0.89]	2.43[1.16]								
TB-ECR:		*	*	*	*	*	*		3.294(108.710)	56.738	.000	8.617	.000	1(33)	19.921	.000
CW	3.24[1.85]	7.03[3.32]	5.06[2.33]	4.27[2.19]	3.80[2.44]	3.66[2.55]	3.49[2.94]	2.59[1.38]								
CCW	4.26[1.74]	12.09[3.16]	8.95[3.22]	8.35[3.19]	8.01[2.87]	7.93[3.00]	7.64[3.18]	3.63[2.97]								

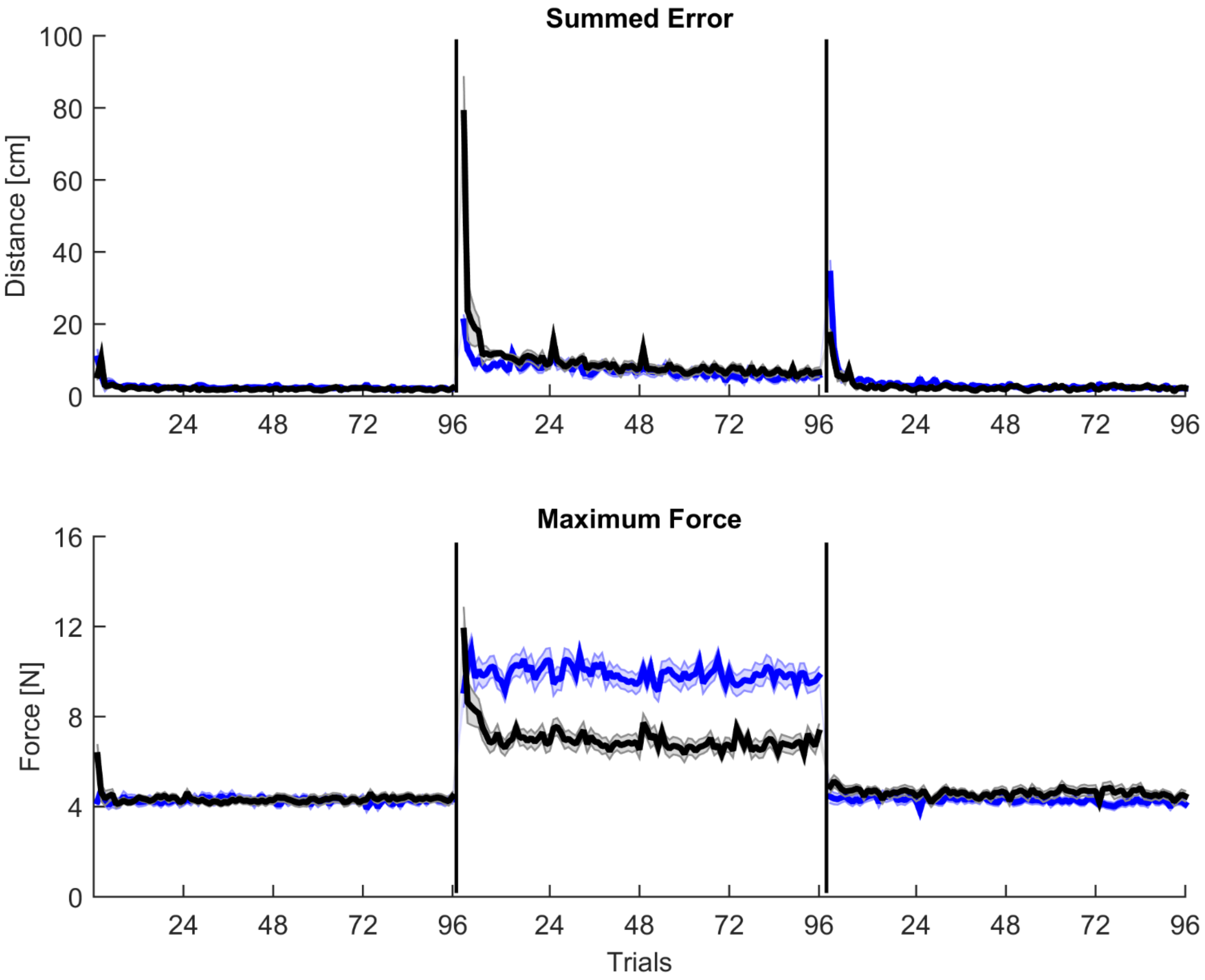
TB-FCR:									3.599(118.763)	35.972	.000	.322	.844	1(33)	2.218	.146
CW	3.33[2.29]	7.64[3.25]	5.97[2.86]	4.92[2.23]	4.66[2.49]	4.47[2.52]	4.46[3.02]	2.48[1.14]								
CCW	4.56[2.16]	8.74[2.02]	6.36[1.96]	5.42[1.72]	5.53[1.77]	5.56[1.69]	5.27[1.93]	3.44[1.87]								
TB-BR:	*			*	*	*		*	3.239(106.880)	34.541	.000	.673	.581	1(33)	12.843	.001
CW	3.53[2.22]	7.87[3.13]	5.97[3.05]	4.902.54]	4.50[2.48]	4.40[2.39]	4.69[3.20]	2.39[1.36]								
CCW	5.28[1.23]	10.0[2.23]	8.37[2.60]	7.62[2.61]	7.63[2.83]	7.47[2.76]	7.13[2.69]	4.79[3.01]								
TB-Bb left:									3.385(111.699)	8.311	.000	2.362	.068	1(33)	.932	.341
CW	2.42[1.73]	4.23[2.59]	3.91[2.74]	3.52[2.54]	2.98[2.35]	2.89[2.39]	3.01[2.77]	1.82[0.47]								
CCW	2.39[0.72]	3.41[2.41]	2.75[1.19]	2.50[1.02]	2.45[1.03]	2.34[0.95]	2.47[1.05]	2.43[1.14]								
ECR-FCR:									2.905(95.879)	46.423	.000	.434	.723	1(33)	1.487	.231
CW	2.65[1.41]	7.41[3.14]	5.83[2.81]	4.70[2.50]	4.55[2.53]	4.28[2.65]	3.92[2.98]	2.13[0.82]								
CCW	3.28[1.41]	8.72[2.88]	6.14[2.43]	5.29[2.26]	5.38[2.44]	5.35[2.41]	4.97[2.40]	2.62[1.79]								
ECR-BR:		*		*	*	*			2.968(97.944)	42.422	.000	2.974	.036	1(33)	11.934	.002
CW	3.04[1.86]	8.00[3.54]	6.14[2.92]	5.26[2.78]	4.79[2.74]	4.61[2.84]	4.22[3.28]	2.38[1.55]								
CCW	3.92[1.94]	12.2[4.28]	9.16[3.39]	8.10[2.77]	8.25[3.71]	7.81[2.99]	7.42[3.36]	3.36[2.70]								
ECR-Bb left:									2.547(84.056)	12.587	.000	1.554	.212	1(33)	.537	.469
CW	1.96[1.34]	4.09[2.66]	3.70[2.78]	3.14[2.40]	2.73[2.48]	2.71[2.72]	2.81[3.29]	1.48[0.45]								
CCW	2.01[0.88]	3.45[2.51]	2.67[1.29]	2.40[0.85]	2.40[0.97]	2.26[1.01]	2.27[1.01]	1.89[1.06]								
FCR-BR:									3.757(123.980)	44.929	.000	2.627	.041	1(33)	1.057	.311
CW	3.17[2.50]	9.15[3.66]	8.23[3.76]	6.78[3.25]	6.74[2.88]	6.01[2.59]	6.31[3.26]	2.21[1.25]								
CCW	3.80[1.62]	8.68[2.70]	6.50[2.23]	5.39[2.05]	5.56[2.30]	5.32[2.01]	4.81[1.99]	3.03[1.73]								
FCR-Bb left:									2.676(88.322)	13.875	.000	5.204	.003	1(33)	3.290	.079
CW	2.16[1.85]	4.51[2.94]	4.64[3.63]	3.99[3.17]	3.41[2.78]	3.16[2.52]	3.36[3.10]	1.45[0.50]								
CCW	2.07[0.60]	3.12[1.45]	2.53[0.97]	2.21[0.80]	2.18[0.79]	2.12[0.81]	2.07[0.75]	1.95[0.99]								
BR-Bb left:									2.735(90.247)	10.602	.000	4.941	.033	1(33)	2.035	.163
CW	2.26[1.99]	4.60[3.05]	4.64[3.94]	4.02[3.31]	3.22[2.64]	3.05[2.74]	3.21[3.41]	1.52[0.58]								
CCW	2.19[0.73]	3.15[1.65]	2.51[1.11]	2.40[0.82]	2.29[0.98]	2.33[1.09]	2.29[1.08]	2.25[1.24]								

Figure Captions

Figure 3.1. Trial-by-trial kinematic evidences of motor adaptation. A trial-by-trial population average (clockwise group, blue line, N = 17; counter-clockwise group, black line, N = 18) profile with shaded standard error for each kinematic measure across the three experimental conditions. Summed error slowly decreases trial by trial during adaptation as expected. Peak force is different between the two groups.

Figure 3.2. Block-by-block muscle-specific activation profiles. For four representative muscles the block-by-block average (clockwise group, blue line, N = 17; counter-clockwise group, black line, N = 18) activation profile (from visual cue to 3 sec afterwards) have been colour coded to describe the evolution of muscle-specific activation over the adaptation period.

Figure 3.3. Block-by-block evolution of co-contraction. For six representative muscle pairs the block-by-block average and standard error of peak co-contraction (clockwise group, blue line, N = 17; counter clockwise group, black line, N = 18) is reported for the two groups. In both groups there is an increase of co-contraction in the beginning of adaptation (Block6), which however decreases bloc-by-block over adaptation, then returning to a low value during wash out.


Summed Error
Distance [cm]
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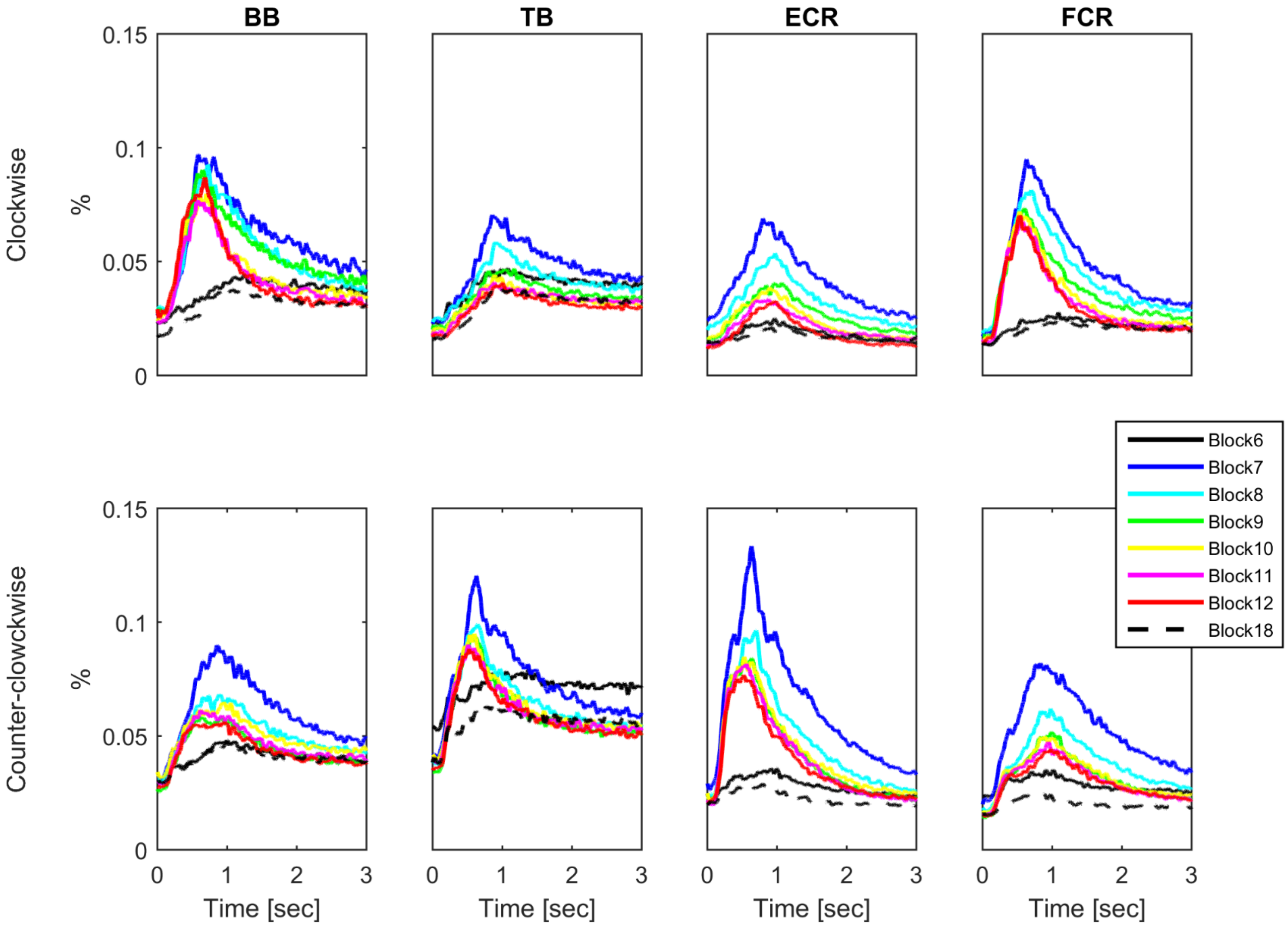
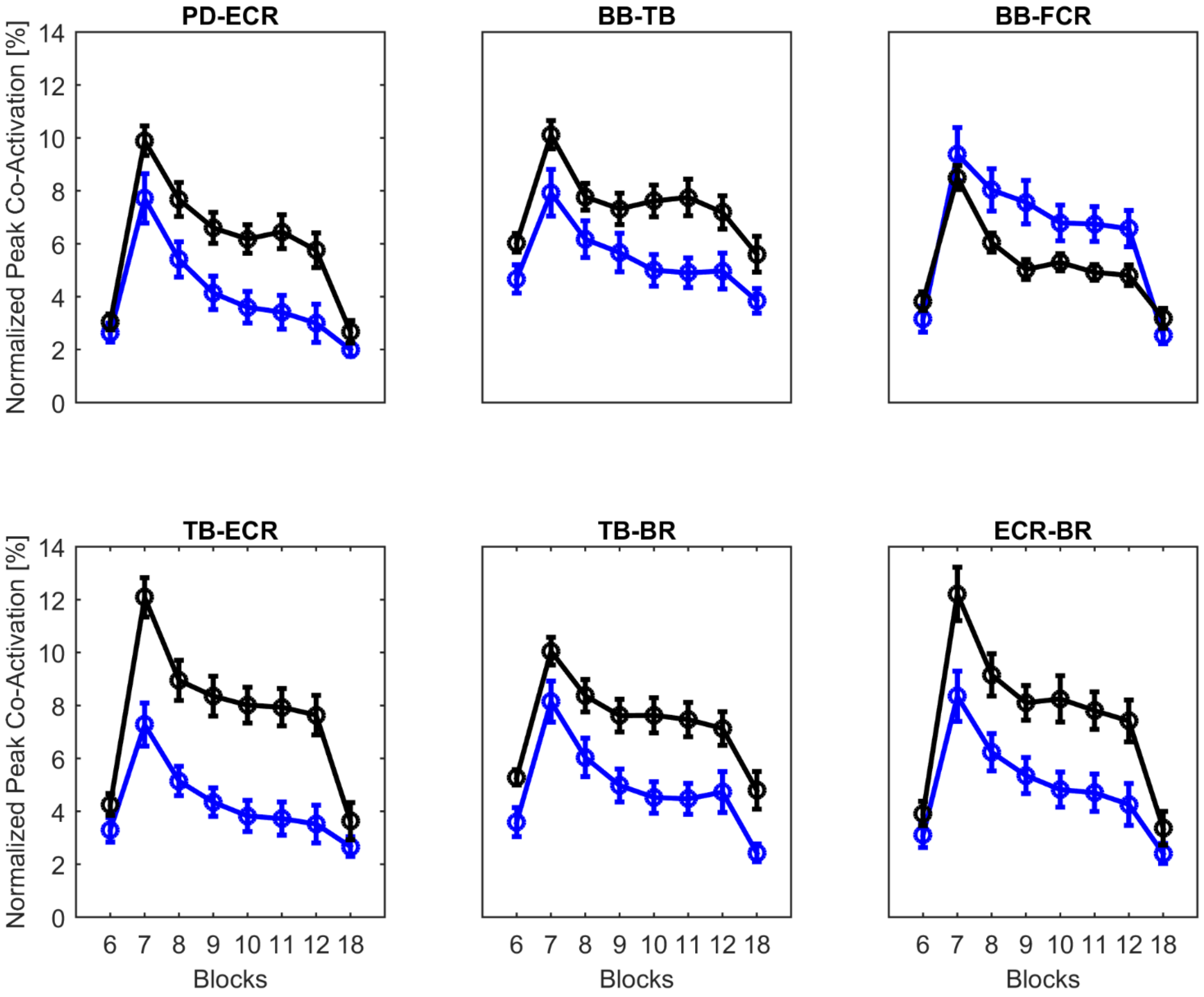
80
60
40
20
0
24
48
72
96
24
48
72
96
24
48
72
96
Maximum Force
Force [N]
16
12
8
4
0
24
48
72
96
24
48
72
96
24
48
72
96
Trials


BB
TB
ECR
FCR
Clockwise
Counter-clowckwise
%
0.15
0.1
0.05
0
0
1
2
3
Time [sec]
Block6
Block7
Block8
Block9
Block10
Block11
Block12
Block18


PD-ECR
BB-TB
BB-FCR
TB-ECR
TB-BR
ECR-BR
Normalized Peak Co-Activation [%]
0
2
4
6
8
10
12
14
6
7
8
9
10
11
12
18
Blocks