Contributions of Cocontraction and Eccentric Activity to Stiffness Regulation

Paula L. Silva1, Sergio T. Fonseca2, Juliana M. Ocarino2,3, Gabriela P. Gonçalves2, Marisa C. Mancini2
1The Center for the Ecological Study of Perception and Action, University of Connecticut, Storrs. 2Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil. 3Centro Universitario de Belo Horizonte (UNI-BH), Belo Horizonte, Brazil.

ABSTRACT. Individuals commonly adjust joint stiffness in response to changes in environmental and task demands. The objective of the present study was to evaluate the contribution of muscular cocontraction and eccentric activity to this adjustment. In all, 30 healthy volunteers participated in the present study. The authors indirectly manipulated elbow stiffness by modifying (a) the frequency of forearm movements (frequency conditions) and (b) the kinetic properties of the forearm through the addition of external mass (mass conditions). Multilevel regression models identified muscular cocontraction and eccentric activity as predictors of joint stiffness in the frequency conditions but not in the mass conditions. Results indicated that cocontraction is not the sole mechanism for stiffness regulation. Rather, the mechanisms that different participants used varied as a function of the demands of the task.

Keywords: elbow joint, electromyography, oscillatory movements

Researchers have observed stiffness modulation during the performance of different activities, such as walking, running, and hopping (Ferris, Liang, & Farley, 1999; Holt, Wagenaar, LaFiandra, Kubo, & Obusek, 2003; Moritz & Farley, 2004). This modulation seems to be a mechanism associated with the adaptation of individuals to the varying environmental contexts in which these activities are performed. For example, when faced with surfaces of different compliances, hoppers and runners adjust leg stiffness accordingly (the higher is the compliance of the surface, the higher is their leg stiffness; Farley, Houdijk, Van Strien, & Louie, 1998; Ferris et al.). Researchers have also reported modulation of joint stiffness in the presence of variations in task demands (e.g., variation in joint load and speed). Holt et al. reported increases in global, vertical, and joint (rotational) stiffness during locomotion as a function of backpack loading, which seemed to minimize lowering of the center of mass. In addition, knee stiffness was directly proportional to running speed (Kuitunen, Komi, & Kyröläinen, 2002). These observations suggest that movement systems make use of stiffness regulation to compensate online for changes in the specific requirements of functional tasks. Our question is whether the specific mechanisms used in the dynamic regulation of joint stiffness vary according to task demands.

The stiffness of a joint is the result of its geometry (Markolf, Bargar, Shoemaker, & Amstutz, 1981) and the stiffness of the tissues surrounding it, such as capsules, ligaments, and muscles (Latash, 1993). The stiffness of a passive tissue is given by its viscoelastic properties and varies nonlinearly as a function of its length. Alternatively, muscle stiffness can be modulated dynamically independently of variations in length through changes in the activation level (Latash). Muscular cocontraction, defined as the simultaneous activation of antagonistic muscles, is the mechanism most commonly proposed for the regulation of joint stiffness (Dorainy, Malfait, Gribble, Towlidkhah, & Ostry, 2004; Holt et al., 2003). The adequacy of this mechanism was demonstrated by the results of studies that reported increases in the stiffness of different joints associated with voluntary increases in the intensity of cocontraction of the muscles acting on them (Garder-Morse & Stokes, 2001).

The significance of the established relation between joint stiffness and muscular cocontraction was reinforced by studies that verified spontaneous increases in the level of cocontraction as a function of greater demands imposed to the joints (Granata & Orischimo, 2001; Lloyd & Buchanan, 2001). For example, increases in the intensity of muscular cocontraction were observed when loads were applied to the spine (Granata & Orischimo), and when the knee joint was subjected to varus–valgus perturbations (Lloyd & Buchanan). Although joint stiffness was not measured directly in these studies, Granata and Orischimo as well as Lloyd and Buchanan have argued that the observed muscular cocontraction constituted a strategy used to regulate joint stiffness, and, consequently, to maintain joint stability in response to the load manipulations. The established relation between cocontraction and joint stiffness underlies the rationale for some training programs to reduce the risk of injury during the performance of functional tasks (Lloyd, 2001). Specifically, researchers have assumed that interventions that produce reduced levels of cocontraction (such as resistance training) are inappropriate to treat and prevent ligament injury (Lloyd). However, this assumption would be unequivocal only if muscular cocontraction was the only mechanism that could be used to modify joint stiffness dynamically.

Despite the argument of different authors that muscular cocontraction is the mechanism used to regulate joint stiffness (Granata & Orischimo, 2001; Lloyd & Buchanan, 2001), there is evidence that it may not be the only one. Obusek (1995) observed increases in global stiffness of the leg during gait that could not be explained by modifications in the intensity of cocontraction of the muscles of the knee and ankle. He suggested that the activity of the triceps surae

Correspondence address: Paula L. Silva, University of Connecticut, The Center for the Ecological Study of Perception and Action, Department of Psychology, 406 Babidge Road, U-1020, Storrs, CT 06269, USA. E-mail address: paula.silva@uconn.edu
muscle opposing the gravitational torque during the stance phase of gait could have been responsible for the observed adjustments in stiffness (Obusek). In this case, the triceps surae muscle would be acting eccentrically, increasing the stiffness of the ankle in the direction opposite to the external torque applied to the joint. This possibility challenges the common assumption that decreases in joint stiffness necessarily result from decreases in cocontraction. However, Obusek did not measure eccentric activation, and therefore the contribution of eccentric muscular activity to the regulation of joint stiffness still needs to be investigated.

Biomechanical models based on pendulum dynamics are used frequently for the evaluation of joint stiffness during the performance of rhythmic movements (Holt et al., 2003; Kugler & Turvey, 1987; Obusek, 1995; Obusek, Holt, & Rosestein, 1995). Critical to our purposes, these models offer predictions about conditions under which joint stiffness is expected to change. For example, based on the escapement-driven hybrid spring-pendulum model—described by Fonseca, Holt, Saltzman, and Fetter (2001)—the frequency of oscillation is determined by the mass and length of the pendulum (representing the oscillating body segment) and by the stiffness of the spring (representing the stiffness of the tissues surrounding the joint about which movement is being performed; Kugler & Turvey). The hybrid spring-pendulum model predicts that movements performed with higher frequencies are associated with higher stiffness, given that the mass and length of the moving body segments are kept constant. Different studies have empirically demonstrated the aforementioned association, lending support to the model’s prediction (Hatsopoulos & Warren, 1996; Latash, 1992).

Modifications in movement frequency do not seem to be the only condition resulting in changes in stiffness. Holt et al. (2003) and Obusek et al. (1995) have performed studies in which increases in stiffness were observed as a result of the addition of masses to the oscillating leg of the participants. Thus, changes in the inertial properties of limb segments (e.g., changes in gravitational torque) may be another condition that requires stiffness modulation. Therefore, joint stiffness can be indirectly manipulated by asking individuals to perform oscillatory movements at different frequencies and with different magnitudes of mass added to their limbs. If joint stiffness and intensity of muscle activation are measured in these different conditions, the relation between joint stiffness and cocontraction or eccentric activity could be determined under different types of demands to the musculoskeletal system.

Specifically, in the present study, we evaluated the contribution of cocontraction and eccentric activity to stiffness regulation of the elbow joint during rhythmic movements of the forearm when variations in the task demands were imposed by (a) modifications in the kinematic characteristics of forearm movements (increases in the frequency of oscillation) and (b) modifications in the kinetic properties of the pendulum (increases in gravitational torque of the forearm and hand segments). Our question is whether these different types of task demands lead to the employment of different mechanisms to regulate joint stiffness. If so, understanding dynamic adjustments of joint stiffness may require consideration of the role that these mechanisms may play in complying with these tasks demands.

Methods and Measures

Participants

Participants were 30 undergraduate students, 15 men and 15 women, with a mean age of 22 years (SD = 1.3 years) and mean body mass of 65.8 kg (SD = 11.2 kg). None of the participants presented musculoskeletal injuries, neuromuscular disorders, or pain in their upper extremities. In order to eliminate the influence of muscle fatigue in the EMG recordings, the participation in physical activities involving the upper extremities up to 48 hr before data collection was established as an exclusion criteria. The procedure of the study was explained to the participants, and informed consent was obtained. This research has been carried out according to the ethical guidelines of the University’s Ethics Review Committee.

Apparatus

In the experimental task, participants performed oscillatory motions of the forearm and hand segments about the elbow, which were registered by an electrogoniometer TSD130 (Biopac System, Inc., Goleta, CA) at a frequency of 1,000 Hz. We used the frequency of oscillation obtained from the goniometer’s output to calculate elbow stiffness. We also used the displacement time series of the forearm yielded by this device to delimit the flexion and extension phases of the cycles of oscillation, which was necessary for the quantification of muscular eccentric activity.

An electromyographer MP100wsw (Biopac System, Inc., Goleta, CA) monitored the activation levels of the biceps and triceps brachi muscles. We used active surface electrodes (TSD150, Biopac Systems, Inc., Goleta, CA) to detect the electrical signals produced by the biceps and triceps brachi muscles. We collected electromyographic data to allow quantification of cocontraction and eccentric activity produced by the aforementioned muscles during the experimental task.

Procedure

On arrival, we weighed the participants and measured the length of their dominant forearms and hands as indicated by Dempster’s anthropometric data (Winter, 1990). We used the anthropometric measures to calculate the participants’ elbow stiffness in each test condition (Fonseca, Holt et al., 2001).

We indirectly assessed stiffness by modeling the arm as an escapement-driven, hybrid spring-pendulum system with viscous damping as described by Fonseca, Holt et al. (2001). Thus, we asked participants to perform rhythmic oscillations of the forearm about the elbow, simulating
the movement of a pendulum. During the oscillations, we recorded the EMG activities of the biceps and lateral head of the triceps muscles at frequencies of 1,000 Hz each. These muscles were selected to represent the activity of the elbow flexors and extensors, respectively (Latash, 1992). After adequate skin preparation, we positioned active electrodes over the area of greatest bulk of these muscles, following the guidelines described by Cram and Kasman (1998). The electrode placement on the elbow flexors did not allow separation of the activity of the long and short heads of the biceps because these two heads mesh at the area of greatest bulk of the biceps. The placement of all electrodes guaranteed optimal EMG activity during contraction of the target muscle and no significant activation during contraction of the target muscle’s antagonist (cross-talk). A ground electrode was positioned over the acromion.

Subsequently, we asked the participants to sit on a chair with their backs supported and to place their dominant arm onto a cushioned armrest (see Figure 1). The armrest supported the distal end of the upper arm, and its height was selected to position the participant’s forearm perpendicular to the ground. We attached the electrogoniometer to the right arm of each participant and then calibrated the electrogoniometer following manufacturer’s instructions. Next, we instructed participants to perform small-amplitude rhythmic movements of their forearm about the elbow joint, with the least possible effort, under the different conditions described subsequently.

Initially, the participants selected a comfortable frequency of oscillation, which required the least possible effort to perform (baseline condition). We instructed them to inform us as soon as they were able to sustain the self-selected frequency. Beginning at this point, the EMG signals and the cycles of oscillation were registered for 20 s. During this period, we observed stability of the selected frequency and minimal EMG activity. We collected five trials and discarded the ones with the highest and lowest mean frequencies. The mean frequency of the three remaining trials was considered the preferred frequency. (The test–retest intraclass correlation coefficient [ICC] of the method used to determine the preferred frequency of the participants was .98.) We used this preferred frequency to calculate elbow stiffness and used the EMG activities of the muscles recorded during the same three trials to compute cocontraction and eccentric activity at the baseline condition.

After participants performed the experimental task in the baseline condition, they performed the experimental task under manipulations of the gravitational torque (mass conditions) and of the frequency of oscillations (frequency conditions) to induce changes in elbow stiffness. To modify the gravitational torque (and consequently manipulate elbow stiffness), we added masses corresponding to 20%, 40%, 60%, 80%, and 100% of the weight of the forearm and hand to the wrist of the participants and instructed them to find a comfortable frequency of oscillation for each mass condition. We randomized the order in which the masses were added.

Following the mass conditions, the participants had a 10-min rest. We then instructed them to oscillate the forearm and hand segments at their preferred frequency (obtained in the baseline condition) and at frequencies 10%, 20%, 30%, and 40% higher than the preferred one. These frequencies were presented to the participants by a metronome. At each frequency condition, we determined the moment at which the participants began to oscillate at the correct frequency. As soon as the participants believed that they could sustain that frequency, we began data collection. We randomized the frequency order, and to guarantee the validity of the stiffness estimates that we obtained using the hybrid pendulum-spring model, frequencies slower than the preferred one were not used (Abe & Yamada, 2003).

Participants performed three trials, at 20 s of oscillation each for the mass and frequency conditions. We used the mean frequency that each participant performed in each condition to calculate joint stiffness. The amplitudes of oscillation monitored during data collection never overcame 18° and were not affected by the experimental manipulations.

The EMG signals of the biceps and triceps muscles obtained during the different experimental conditions were normalized by their maximal voluntary contraction (MVC). During the MVC evaluations, participants sat with their back and dominant arm supported in the same way that we described for stiffness evaluation. The participants’ elbow was positioned at 15° and 120° of flexion for triceps and biceps brachii evaluations, respectively. We instructed the participants to perform three maximum isometric contractions of each
muscle with durations of 6 s each, recorded EMG signals from the target muscle during the 6 s of contraction, and selected the 2 s during which the highest intensity of EMG activity was produced in each trial for analyses. We used the contraction of each muscle that generated the greatest EMG activity in the normalization procedure.

**Data Reduction**

The oscillatory movements of the forearm and hand segments about the elbow were modeled by an autonomous escapement-driven hybrid spring-pendulum with viscous damping (Fonseca, Holt, et al., 2001). This model implied that a forcing moment is required to maintain the oscillations because of the small damping coefficient. Researchers assumed that this force acts on the center of mass of the system for a short period of time and at a limited portion of the cycle, resembling the escapement mechanism of a pendulum clock (Fonseca, Holt, et al.). The mechanism of an escapement is to release energy once per cycle to replace the energy lost, such that a steady oscillatory behavior is achieved. An important characteristic of this clock-like behavior is that the forcing can change the amplitude of oscillation but allows the system to maintain its natural frequency (Holt, Fonseca, & LaFiandra, 2000). More specifically, the amplitude of a hybrid spring-pendulum system is directly proportional to the forcing and inversely proportional to the amount of damping present. Alternatively, the frequency of oscillation is close to the linear natural frequency, which is determined by the mass and length of the pendulum and the stiffness of the spring. This has been true for angular amplitudes smaller than 20° (when the angle in radians is equal to the sine of the angle and the cosine of the angle in radians is approximately equal to one). For such amplitude range, a pendulum has a constant linear stiffness, and the frequency of oscillations is not affected by changes in amplitude. Because in the present study the amplitude of oscillation did not overcome 18°, the assumption of constant linear stiffness throughout the movement cycle was reasonable.

An autonomous escapement-driven oscillator demonstrates angular displacements with a single frequency component in its power spectrum, which indicates harmonic motion (Fonseca, Holt et al., 2001; Holt et al., 2000). In cases of harmonic motion, the observed frequency can approximate the system’s natural or resonant frequency. If the mass and length of the pendulum are known and the frequency can be observed, stiffness can be calculated as

\[ k b^2 = ((mL_e^2)(\omega^2)) - mL_g \]  

(1)

where \( kb^2 \) represents the elastic torque produced by the spring. Because \( b \) (distance from the axis of rotation to the attachment of the spring) is a constant in the model, any modification in the elastic torque represents modifications in the stiffness \( k \) of the tissues surrounding the joint and consequently joint stiffness. According to Equation 1, to calculate elbow stiffness in the present study, the values of the frequency of oscillation (\( \omega \)), mass (\( m \)), and length (\( L_e \)) of the simple pendulum equivalent to the pendulum comprising the forearm and hand are necessary. We obtained these three values for each participant in the baseline condition and in the frequency and mass conditions.

We obtained the frequency of oscillation on the baseline, mass, and frequency conditions from the displacement time series registered using the electrogoniometer. The mass of the simple pendulum equivalent (\( m \)) is the sum of the masses of the forearm and hand estimated from total body mass using Dempster’s anthropometric data (Winter, 1990) and the added external mass when that was the case. We calculated the length of the simple pendulum equivalent (\( L_e \)), the distance from the center of mass of the forearm, and hand complex to the elbow axis, using the parallel axis theorem. To perform this calculation, we had to estimate the total mass of the forearm–hand complex and the center of mass of each segment from total body mass and segment lengths, using Dempster’s anthropometric data (Winter).\(^2\) The gravitational torque of the simple pendulum equivalent was the product of \( m, L_e \), and the gravitational acceleration. More details regarding these calculations can be found elsewhere (Kugler & Turvey, 1987; Obusek et al., 1995).

We performed EMG data processing using the software Acqknowledge. The EMG signals of the biceps and lateral head of the triceps were full-wave rectified and, subsequently, low- and high-pass filtered with cutoff frequencies at 10 and 500 Hz, respectively. We calculated the root mean square (RMS) of the signals produced by each muscle during the MVC tests. The values we obtained were a measure of the intensity of activation. We used the highest RMS value obtained from each muscle during the MVC tests to normalize the EMG signals registered during the stiffness evaluations. The resulting output from the normalization procedure quantified the intensity of biceps and triceps activation registered during the oscillations as a percentage of their maximal activation. Such normalization procedures render the EMG recordings comparable between muscles and among participants.

We used the normalized EMG signals to calculate the study variables of total eccentric activity (TEA) and cocontraction. Prior to the calculation of TEA, we divided the cycles of oscillation in two alternating phases: flexion and extension. We obtained the intensity of eccentric activation of the biceps muscle (ECC\textsubscript{biceps}) by averaging the normalized EMG activity produced by this muscle at each sampled time point during elbow extension. Similarly, triceps eccentric activity (ECC\textsubscript{triceps}) was quantified by averaging the normalized EMG activity produced by this muscle at each sampled time point during elbow flexion. TEA was calculated by adding ECC\textsubscript{biceps} and ECC\textsubscript{triceps}.

**Muscular cocontraction** was operationally defined as the simultaneous activation of the biceps and lateral head of the triceps. Following such definition, we obtained a cocontraction index (CCI) by quantifying the area of overlap.
between the EMG signals of the biceps and triceps. We obtained this overlapping area by taking the minimal value of the two normalized signals at each sampled time point and integrating them across the total trial time. This method was proposed and described by Unnithan, Dowling, Ayub, and Bar-or (1996) and demonstrated a test–retest ICC of .96 (Fonseca, Silva, Ocarino, & Ursini, 2001).

It should be noted that EMG activity is not a measure of muscle torque, especially during dynamic conditions. Muscle torque is not only determined by muscle activation, but also by other factors, such as muscle moment arm and muscle length, which vary at different points in the range of motion. Hence, the EMG measures reported in the present study should only be seen as indicators of changes in the resistance of evaluated muscles to joint movement and not as the isolated causes of these changes.

**Statistical Analyses**

We calculated means and standard deviations of the variables of elbow stiffness, muscular cocontraction, and TEA in the baseline and in each experimental condition. Within-subject linear regression analyses tested the association between gravitational torque of the simple pendulum equivalent and elbow stiffness in each participant. We performed these analyses to guarantee that the manipulation of elbow stiffness through modifications of gravitational torque was efficient in every participant.

We used multilevel models for repeated-measures design (or random effect models; Laird & Ware, 1982) to test whether the variables, cocontraction and TEA, were significant predictors of the outcome variable elbow joint stiffness in the mass and frequency conditions. The choice of this analysis was on the basis of two factors. First, standard multiple regression assumes that observations are independent. In the present study, we performed measurements on each participant under multiple conditions, clearly violating this assumption. Fitting a model that does not recognize the dependence between measures may create technical problems such as underestimation of standard errors of regression coefficients and a consequent increase in the chance of incurring a type I error. Multilevel models incorporate the dependence among measures leading to more accurate standard error estimates. Hence, it constitutes a more conservative analysis. A second advantage of using multilevel modeling is that this analysis not only tests the association among the study variables, but also informs whether the pattern of association varies from individual to individual. Thus, this analysis provides a more comprehensive view of the data by modeling processes in its multiple levels (in the present case, the global group level and the individual participant level).

The multilevel regression model of the present study has joint stiffness as the outcome variable and cocontraction and TEA as predictors. In order to fit repeated-measures data using a multilevel model, we considered the individual measurements as the Level 1 unit and the participants as the Level 2 unit as follows: Level 1, $S_{ij} = \beta_0 + \beta_1(CCI)_{ij} + \beta_2(TEA)_{ij} + e_{ij}$ where $S_{ij}$ is the stiffness value of the $i$th condition of the $j$th participant; $\beta_0$ is the intercept for the $j$th participant; $\beta_1$ is the slope coefficients for the CCI for the $j$th participant; $\beta_2$ is the slope coefficient for TEA for the $j$th participant; and $e_{ij}$ is the random departure of the $i$th condition of the $j$th participant from his or her predicted line (within-subject variability). For Level 2, $\beta_0 = \beta_1 + \mu_{ij1}$, $\beta_2 = \beta_1 + \mu_{ij2}$

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**TABLE 1. Means and Standard Deviations of Variables of Stiffness, Cocontraction, and Total Eccentric Activity (TEA) in Six Mass Conditions and Five Frequency Conditions**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Stiffness (N-m)</th>
<th>Cocontraction, MVC (%)</th>
<th>TEA, MVC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$M$</td>
<td>$SD$</td>
<td>$M$</td>
</tr>
<tr>
<td>Mass (%)$^a$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>1.35</td>
<td>1.09</td>
<td>0.021</td>
</tr>
<tr>
<td>20</td>
<td>2.83</td>
<td>1.60</td>
<td>0.022</td>
</tr>
<tr>
<td>40</td>
<td>3.99</td>
<td>2.07</td>
<td>0.024</td>
</tr>
<tr>
<td>60</td>
<td>5.40</td>
<td>3.12</td>
<td>0.025</td>
</tr>
<tr>
<td>80</td>
<td>6.70</td>
<td>3.76</td>
<td>0.027</td>
</tr>
<tr>
<td>100</td>
<td>8.18</td>
<td>3.84</td>
<td>0.027</td>
</tr>
<tr>
<td>Frequency (%)$^b$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preferred frequency</td>
<td>1.35</td>
<td>1.09</td>
<td>0.022</td>
</tr>
<tr>
<td>10</td>
<td>2.38</td>
<td>1.45</td>
<td>0.025</td>
</tr>
<tr>
<td>20</td>
<td>3.40</td>
<td>1.72</td>
<td>0.027</td>
</tr>
<tr>
<td>30</td>
<td>4.68</td>
<td>2.14</td>
<td>0.028</td>
</tr>
<tr>
<td>40</td>
<td>6.01</td>
<td>2.62</td>
<td>0.032</td>
</tr>
</tbody>
</table>

Note. MVC = maximal voluntary contraction.

$^a$Percentage of the sum of the forearm and hand masses.

$^b$Percentage of the preferred frequency.

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**Contributions of Cocontraction**
respectively, for the coefficient for cocontraction, and slope coefficient for TEA, the mean (between-subject variability) of the intercept, slope coefficient for cocontraction, and slope coefficient for TEA, respectively, for the \( j \)th participant.

As can be seen, the intercepts and slope coefficients for cocontraction and TEA are estimated for each participant. The mean slope coefficients for cocontraction and TEA are the fixed effects of the model and are used to test whether cocontraction and TEA are predictors of joint stiffness at the group level, considering both within- and between-subjects variance for standard error estimation. The random effects are the within- and between-subject variances.

Significant between-subjects random effects indicate the presence of significant differences between the intercepts or slopes estimated for each participant. In the present study, the presence of such random effects suggests individual variability in the mechanisms related to stiffness regulation. Thus, in the case of significant between-subject random effects, we used within-subject linear regression analyses with the sole purpose of describing such variability. These analyses yielded the individual associations between stiffness and each of the predictors (cocontraction and TEA) and, consequently, allowed us to describe the mechanism related to stiffness regulation in each participant and experimental condition.

**Results**

The means and standard deviations of the variables of stiffness, cocontraction, and TEA in the six mass conditions and in the five frequency conditions are presented in Table 1. The higher standard deviation in the 40% and 80% mass conditions can be attributed to the atypically high magnitude of TEA presented by 1 participant in these two conditions. The results of further analyses include this participant because excluding him did not produce any qualitative changes in the results.

The within-subject linear regression analyses demonstrated significant correlations between joint stiffness and gravitational torque of the arm in each participant. The correlation coefficients varied from .88 to .99. In addition, the analyses of the cycles of oscillation demonstrated that the participants of the present study were able to follow the frequencies presented by the metronome, with a maximum error of 2%. Therefore, the manipulations of joint stiffness through the addition of masses to the forearm (mass conditions) and through increases in frequencies of oscillation (frequency conditions) were efficient in every participant.

The frequencies observed in all experimental conditions varied from .91 to .92 Hz \((M = 1.25 \text{ Hz}, \ SD = 0.22 \text{ Hz})\). According to Hatsopoulos and Warren (1996), linearity is a reasonable assumption in this frequency range, which reinforces the adequacy of the linear model used in the present study to estimate joint stiffness.

**Mass Conditions**

**Multilevel Model**

The multilevel regression model revealed that the variables of cocontraction and TEA were not significant predictors of joint stiffness in the mass conditions (see Table 2). However, the results revealed a significant intercept variance. That is, significant differences were observed among the intercepts of the regression lines estimated for each participant.

**Within-Subject Linear Regressions**

The linear regression analyses performed with the variables of cocontraction and joint stiffness resulted in correlation coefficients that varied from .11 to .99 \((M = .56, SD = .31)\). Cocontraction was significantly correlated with joint stiffness in 11 participants \((r > .85, p < .05)\). This finding suggests that some participants used cocontraction to regulate elbow stiffness. The remaining 19 participants presented correlation coefficients between cocontraction and joint stiffness that were not significant. Of the 19 participants, 17 showed \(r \leq .5\), and 2 showed \(.5 < r \leq .7\).

When the association between joint stiffness and TEA was tested in the same participants, the correlation coefficients varied from .10 to .98 \((M = .53, SD = .21)\). In all, 26 participants presented nonsignificant correlation coefficients. Of these participants, 21 showed \(r \leq .5\), and 5 showed \(.5 < r \leq .7\). In only 4 participants, TEA was significantly correlated with joint stiffness \((r > .9, p < .05)\). In summary, the two sets of within-subject regression analyses showed that elbow stiffness was significantly correlated with cocontraction in 11 participants and with eccentric activity in 4 others. In addition, 15 participants did not seem to have used, as a preferred strategy, any of the two mechanisms evaluated. Cocontraction or TEA explained less than 25% of the variance \((r^2 \leq .25)\) in most of the latter participants.

**Frequency Conditions**

**Multilevel Model**

The multilevel analysis demonstrated that cocontraction \((p = .013)\) and TEA \((p = .001)\) were significant predictors of the variable joint stiffness in the frequency conditions (see Table 2). In addition, significant differences among the slopes and intercepts of the regression lines estimated for each participant were identified \((p < .0001)\).

**Within-Subject Linear Regression Analyses**

The correlation coefficient between cocontraction and the variable joint stiffness varied from .14 to .99 \((M = .67, SD = .28)\). In 11 participants, cocontraction was significantly correlated to elbow stiffness \((r > .91, p < .05)\). In the other 19 participants, this correlation was not significant \((13 \text{ participants showed } r \leq .5, \text{ and } 6 \text{ showed } .5 < r \leq .7)\).

The association between joint stiffness and TEA was also tested in the 30 participants. The correlation coefficients
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obtained varied from .12 to .98 (M = .83, SD = .21). In all, 20 participants presented significant correlations (r > .92, p < .05), but in 10 of them, TEA was not significantly correlated to joint stiffness. Of the latter 10 participants, 2 showed r ≤ .5, and 8 showed .5 < r ≤ .7. In summary, in 17 participants, TEA was identified as a significant predictor of joint stiffness, whereas cocontraction was a significant predictor in 7 other participants. In 4 of the participants, stiffness was correlated with cocontraction and TEA. In 3 other participants, neither of the mechanisms accounted for more than 50% of the variance in elbow stiffness (r² ≤ .7).

The individual analyses showed that although most participants used active mechanisms to regulate stiffness in the frequency conditions (cocontraction or eccentric activity), passive mechanisms were more prevalent in the mass conditions. A minority of participants did show correlation between joint stiffness and the neuromuscular mechanisms in the mass conditions. However, the correlation coefficients between joint stiffness and CC and TEA were smaller in the mass conditions than in the frequency conditions, t(29) = 2.06, p = .048, and t(29) = 4.65, p < .001, respectively. Hence, the results of the individual analyses are consistent with the multilevel model, which identified both CC and TEA as significant predictors of stiffness in the frequency conditions, but not in the mass conditions.

### Discussion

The results of the present study demonstrated that, even though elbow stiffness was consistently regulated as a result of increases in joint load and movement frequency, there was considerable variability in the strategies participants used for this regulation. Despite the observed variability, it was possible to identify preferred strategies for stiffness regulation in the mass and frequency conditions.

When elbow stiffness was manipulated through addition of masses to the forearm, neither cocontraction nor TEA was identified as a significant predictor of elbow stiffness by the multilevel model. There are two possible explanations for this finding. First, the neuromuscular mechanisms evaluated were based only on the activation patterns of the biceps and lateral head of the triceps brachi muscles. Therefore, it is possible that other elbow flexors and extensors, which were not evaluated in the present study, modified their activation in response to the addition of masses. However, Latash (1992) observed a high correlation between activity of the biceps and brachioradialis and between the medial and lateral heads of the triceps brachi during oscillations of the forearm about the elbow joint. Thus, a second and more probable explanation for the absence of significant association of elbow stiffness with cocontraction or TEA would be the contribution of passive structures to the regulation of joint stiffness in the mass conditions. More specifically, the observed increases in elbow stiffness may have resulted from amplification in the passive tension of the periarticular tissues, generated by the traction exerted by the masses attached to the wrist.

Many studies have shown that significant modifications of joint stiffness can occur, in the absence of muscular activation, as result of changes in the passive tension offered by periarticular tissues (Chelboun, Conatser, & Giesey, 1997; Cholewicki & McGill, 1996; Weiss, Kearney, & Hunter, 1986). For example, Weiss et al. observed greater values of ankle stiffness when the joint was positioned at the extremes of its range of motion than when it was positioned...
The within-subjects regression analysis showed that cocontraction was the most frequently identified predictor of joint stiffness among the participants that modulated muscular activity. This finding may be related to the need to counteract the traction exerted in the elbow joint by the added loads. In individuals with lower passive stiffness, the addition of masses to the wrist has the potential to cause a more pronounced separation between joint surfaces because of a greater deformation of the tissues around the joint. In this case, cocontraction, through its resultant compressive joint force, would not only complement the passive adjustments in joint stiffness, but would also approximate the joint surfaces, contributing to joint stability. Thus, the stability demands of a specific task, and the musculoskeletal properties available to perform it seem to be related to the intensity of muscular activation and the selection of a specific mechanism to regulate joint stiffness.

In contrast to the mass conditions, the regulation of joint stiffness associated with increases in movement frequency was obtained preferably by modulation of muscular activity. The multilevel model demonstrated that cocontraction and TEA were significant predictors of joint stiffness. This model has also identified differences among the intercepts and the slopes of the regression lines estimated for each participant, which may indicate differences in the passive stiffness and in the efficiency of the mechanisms used, respectively.

The within-subject regression analyses showed that TEA was the most commonly identified predictor of elbow stiffness in the frequency conditions. There are at least two possible explanations for this finding. First, cocontraction was not necessary to approximate the joint surfaces because no traction was applied to the arm. Second, TEA is a more efficient mechanism to regulate joint stiffness because muscular activity is complementary to passive forces (e.g., gravitational and elastic torques) involved in the movement (Schenu & van Soest, 1996). In this case, the activity of the muscles is adjusted only in the direction opposing joint movement, which varies at different points of the movement cycle.

Although TEA was the mechanism most commonly observed in the frequency condition, cocontraction was a significant predictor of joint stiffness in some participants. As opposed to TEA, this mechanism results in a multidirectional increase in stiffness (Osu, Burdet, Franklin, Milner, & Kawato, 2003). As a result, cocontraction involves a higher energetic cost than TEA because the muscle action does not necessarily complement to the action of external, nonmuscular forces involved in the movement (Milner, 2002). However, cocontraction seems to be a simpler strategy for the regulation of joint stiffness precisely because it does not require attunement to the effect of external forces. It is possible that the participants with greater difficulty in following the frequency presented by the metronome used this mechanism. This proposition can be supported by studies that demonstrated a decrease in the intensity of cocontraction associated with gains in ability to perform a specific task (Van Emmerick, 1992; Vincken & Denier van der Gon, 1985). Van Emmerick suggested that with practice, generalized cocontraction is replaced by more efficient muscular strategies that respond specifically to the forces involved in the task. Therefore, practice in a particular activity may lead to the emergence of more refined mechanisms for the regulation of joint stiffness.

In the present study, the mean intensity of cocontraction and TEA did not overcome 0.3% and 3.0% of MVC, respectively. One may argue that this intensity of muscular activation would not be sufficient for stiffness regulation. However, there is evidence that low levels of cocontraction are sufficient to promote stability through its effects on joint stiffness (Cholewicki & McGill, 1996; Cholewicki, Panjabi, & Khachatryan, 1997). For example, Cholewicki et
al. demonstrated that cocontraction of 2–3% of MVC could significantly affect spinal stiffness and promote spinal stability, even at its neutral position, in which the passive tension in the tissues is minimal. Therefore, it is possible that the levels of cocontraction and TEA observed in the present study were sufficient to significantly contribute to the regulation of elbow stiffness and, consequently, to the performance of the oscillatory task under the different types and levels of demand imposed.

Stiffness was assessed indirectly by modeling the arm as an escapement-driven hybrid system. This model has been used in a number of studies and has the advantage of allowing the dynamic evaluation of stiffness without disrupting the movement (Fonseca, Holt, et al., 2001; Holt et al., 2000; Holt et al., 2003). Its main assumption is that the observed movement frequency is consistent with the resonant frequency of the system. Hatsopoulos and Warren (1996) tested this assumption and demonstrated that the selected frequency of oscillation of the forearm about the elbow joint agreed with the empirically determined resonant frequency of the muscle-limb complex, as proposed by Kugler and Turvey (1987). In addition, Latash and Gottlieb (1991) showed that when individuals were required to perform rhythmic movements at a specific frequency, they modulate joint stiffness so as to keep the resonant frequency of the system close to the required one. Such modulation has been shown to result in a decrease in the required torque to produce the movement (Latash, 1992), minimization of metabolic cost (Holt, Hamil, & Andres, 1991), maximization of stability of movement pattern, and simplification of control (Goodman, Riley, Mitra, & Turvey, 2000). Last, Holt et al. (2003) showed that the estimates of global stiffness from the model were qualitatively the same as more direct measures (e.g., vertical stiffness, rotational stiffness). The research reviewed previously not only provided empirical support for the model’s assumption, but also showed the functional advantages of a system working in resonance.

However, it is important to note that not all movements occur in resonance. For example, Abe and Yamada (2003) showed that the observed frequency of oscillation of the forearm about the elbow is close to the resonant frequency only when the oscillations are performed at the preferred frequency or faster. Hence, the use of hybrid pendulum-spring models to characterize rhythmic movements performed below the preferred frequency of oscillation is questionable.

Another underlying assumption of these models is that a large number of spring-like structures (e.g., muscles, tendons, other connective tissues) affecting joint motion can be represented by a single spring. The stiffness of this single spring is equated with the global (joint) stiffness of the modeled system, which is assumed to be linear and constant throughout the range of motion, regardless of variation in the activation (and, hence, in the stiffness) of individual muscles. In other words, it is assumed that, despite the evident complexity of the neuromuscular system, the collective behavior of individual muscles and other soft tissues results in a type of oscillation that is consistent with a linear pendulum-spring system.

Striking support of the latter assumption has accumulated throughout the years. For example, the leg swing about the hip during gait has been modeled as a pendulum, with the soft tissues (muscles, tendons, ligaments) acting as one global spring (Holt et al., 1990; Holt, Jeng, & Fetters, 1991; Holt, Jeng, Ratcliffe, & Hamil, 1995; Kugler & Turvey, 1987; Turvey, Schmidt, Rosenblum, & Kugler, 1988). These models have been shown to effectively predict the preferred walking frequencies of humans, bipeds, and quadrupeds. In addition, pendulum-spring models have been successfully used to capture gait parameters of individuals with neurological impairment (Fonseca, Holt, et al., 2001; Ulrich, Haehl, Buzzi, Kubo, & Holt, 2004). Therefore, even though biomechanical models used to estimate stiffness do not inform about the properties of individual structures involved in the movement, they seem to reflect their overall impact in behavior.

As may be expected, the assumption of a constant, linear stiffness does not hold universally. For example, Bennett, Hollerbach, Xu, and Hunter (1992) showed that stiffness is time-varying in large amplitude rhythmic movements of the forearm and could not be captured in such circumstance by a strictly linear model. This assumption is also not warranted when the frequency of oscillation is greater than 2 Hz (Hatsopoulos & Warren, 1996). As noted, the assumption of linear stiffness is reasonable in the present study given the range of amplitude and frequency of our experimental task (see Methods and Measures section). Therefore, our use of the escapement-driven hybrid pendulum-spring model to estimate stiffness is justified.

A limitation of the present study was that the activity used to manipulate elbow stiffness presented lower force production demands than that of the majority of functional activities. This low demand could be an explanation for the absence of association between joint stiffness and the neuromuscular mechanisms assessed in the mass conditions. The reduction in elbow joint congruency generated by the addition of masses to the forearm possibly had a lower impact on joint stability during the performance of the oscillations than it would have had in most daily and sports activities.

The study of more functional activities, involving multiple body segments, possibly reveals even more refined mechanisms involved in the regulation of joint stiffness. For example, Farley et al. (1998) observed increases in ankle stiffness during hopping that could not be explained by modifications in the activation level of the tibialis anterior or triceps surae muscles. Farley et al. suggested that changing limb geometry could affect joint stiffness because it modifies the length of the muscle-tendon unit and in turn its passive stiffness. Moreover, there is evidence that forces that arise during movement may also play a role in the adjustment of limb stiffness, independent of changes in cocontraction or limb geometry (Doran, Towhidkhah, & Osty, 2007). Specifically, Dorainy et al. observed differences in arm stiffness estimated during postural maintenance and
movement in the same location of the workspace (i.e., limb geometry was the same in the two conditions). Simulation of the experimental procedure showed that even when the modeled cocontraction levels were equivalent in posture and movement, the empirically observed differences in arm stiffness were replicated. Therefore, the mechanisms identified in the present study are certainly not the only possible strategies used in the regulation of joint stiffness.

That cocontraction is not the sole mechanism involved in stiffness regulation has implications for rehabilitation. More specifically, decreased levels of muscular cocontraction during the performance of motor activities have frequently been taken as indicative of deficits in the regulation of joint stiffness leading to deficits in dynamic stability (Lloyd, 2001). However, the present study showed that dynamic cocontraction should not be defined as the sole index of such deficits. Other mechanisms, such as eccentric muscular activity, may be in effect and should be considered.

The activity performed in the present study, despite its limitations, allowed the evaluation of the contribution of cocontraction and TEA in the regulation of joint stiffness and the identification of situations in which they are preferably used. In addition, it was possible to capture the great individual variability involved in this regulation. Therefore, it is likely that there is no unique neuromuscular mechanism that is used consistently to regulate joint stiffness, even when simple tasks are performed. The specific mechanism used by each individual is possibly an emergent, context-dependent strategy. In other words, given the task and the musculoskeletal properties available to perform it, the most adequate available mechanism is used to regulate joint stiffness in each specific context.

Conclusion

The results of the present study demonstrated that cocontraction is not the sole neuromuscular mechanism involved in the regulation of joint stiffness. We have shown that eccentric activity not only is an alternative mechanism for such regulation, but also is the most frequently used one under certain task constraints (e.g., variations in the frequency of oscillation). In addition, in the mass conditions, most participants increased joint stiffness despite the absence of modification of the intensity of muscular activity, which underscores the relevance of passive structures in joint stiffness regulation. Last, even though preferable mechanisms were identified in the mass and frequency conditions, the variability we observed suggests that other factors (e.g., passive stiffness, practice in a particular task) may be related to the mechanism used. Hence, understanding the role of neuromuscular mechanisms in stiffness regulation requires a careful consideration of the interplay among individual’s musculoskeletal resources and capabilities and the demands of the task.

NOTES

1. Stiffness can be generally understood as the resistance of a structure (e.g., a biological tissue, joint, or limb) to deformation or deflection secondary to an applied force. With respect to biological tissues (i.e., muscles, tendons, other connective tissues), stiffness can be quantified as the changes in force divided by the resultant deformation. Joint stiffness, being analogous to the concept of rotational stiffness, can be obtained by dividing the change in joint torque applied to a joint by its corresponding angular displacement (Holt et al., 2003). Last, the stiffness of a limb (e.g., leg stiffness) is a more global measure that reflects the resistance offered by the different joints composing the limb to changes in their angular position. For example, Farley et al. (1998) derived leg stiffness, during the stance phase of gait, from the ratio of peak reaction force and peak compression of the leg spring. Compression of the leg spring is related to the resistance of the different leg joints to being flexed by the body weight during load acceptance in the stance phase of gait.

2. Dempster’s equations used to estimate the inertial properties of limbs are based on methods of segmentation of cadavers, which have a number of limitations (e.g., nonidentity of postmortem and living tissues, displacement of tissue during segmentation). Errors in the estimation of limb properties transfer to stiffness calculations. Because there is no gold standard method to estimate these properties, such errors cannot be known precisely. However, the estimates obtained in the present study are not different from the ones obtained with other methods (Chandler, Clauser, McConville, Reynolds, & Young, 1975; Clauser, McConville, & Young, 1969; Zatsiorsky, Seluyanov, & Chugunova, 1991). In addition, because of the present study’s repeated-measures design, any error in stiffness estimation is constant across conditions for each participant. The latter argument holds because we used a linear model to estimate stiffness in the present study. Hence, the changes in stiffness as a function of our manipulation are reliable despite expected errors in its absolute magnitude.

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Conclusions of Cocontraction


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