From Tremor to Movement: Differences in Variability and Coupling During Bilateral Finger Actions

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This study examined changes in movement variability, coupling, and muscle activity across three different bilateral finger movements (e.g., postural, isometric, and isotonic). It was predicted that movements characterized by increased inter-limb coupling would be associated with increased levels of muscle activity and reduced movement variability. The results demonstrated task-specific differences in inter-limb relations with coupling being lowest during postural tasks and highest under isotonic conditions. However, a similar pattern was not observed for muscle activity and movement variability. Of the three tasks, postural tremor movements were more variable and had lower levels of muscle activity. Alternatively, increased muscle activity and more regular movement dynamics were seen under isometric conditions. Overall, it would appear that differences in bilateral coupling across tasks are not reflective of a single driving mechanism but rather reflect differential contribution from intrinsic neuromuscular and mechanical sources.

Keywords: Coupling, Variability, Bilateral, Muscle, Tremor

Variability of motion is widely considered as an intrinsic and essential characteristic of many everyday movements, affording the sensoriomotor system greater flexibility in responding to various perturbations and stresses (Yates 1987; Yates 1988; Bassingthwaighte et al. 1994; Neuringer et al. 2000; Neuringer 2002). However, there are limits to the degree of variability for many actions, as individuals will tend to produce actions with highly predictable dynamics, even when instructed to move in a random fashion (Newell et al. 2000a; Newell et al. 2000b; Deutsch and Newell 2004; Morrison et al. 2007). While specific movements can appear to be highly variable, this description is largely subjective since all actions are bounded by both the neuromuscular and mechanical components (degrees of freedom, df’s) of the human system and also by the nature of any interaction or coupling between these specific movement components (Kugler and Turvey 1987; Mitra et al. 1998; Vaillancourt and Newell 2002a). The available df’s for a given movement and the manner in which these elements are coupled both make major contributions to the
resultant variability of the movement (Vaillancourt and Newell 2002a; Vaillancourt and Newell 2002b; Kyriazis 2003).

Bilateral movements represent a convenient method for investigating the relations between coupling and variability as such movements are characterized by discrete patterns of coordination (von Holst 1973; Haken et al. 1985). For example, during rhythmic, bilateral isotonic actions, the coupling relation between the two homologous effectors tends to be strong, irrespective of whether the movement is performed in a coincidental (in-phase) or alternating (out-of-phase) fashion (Kelso 1984; Kelso 1994; Carson 1995; Carson 2005). Further this pattern of coordination is often preserved across different limb combinations, movement tasks and/or planes of motion (Carson 1995; Swinnen et al. 2001; Carson and Kelso 2004; Levin et al. 2004; Li et al. 2004). However, a similarly strong pattern of coupling is not the norm for other bilateral actions. For example, the reported strength of the coupling relation during isometric actions, while high (Heuer 1993; Morrison and Newell 1998; Steglich et al. 1999; Boonstra et al. 2007), these levels do not appear to approach that reported within isotonic studies (Carson 1995; Carson 2005; Morrison and Sosnoff 2009). Further, during postural tremor activities, where individuals are simply required to hold their arms against gravity, the two limbs exhibit a high degree of independence (Marsden et al. 1969; Morrison and Newell 1999). Indeed, it would seem that a lack of interlimb relations is the standard for tremor production in healthy individuals since this relation is unaffected by fatigue (Morrison et al. 2005) or the normal process of aging (Marshall 1961; Morrison et al. 2006). Based upon these studies, a relevant question is whether there is any pattern to the change in interlimb coupling across different tasks. One possibility is that the changes in coupling seen across different movements form a systematic pattern or continuum, ranging from postural (tremor) actions, which exhibit no coupling, to isometric and isotonic movements which are characterized by stronger interlimb relations.

Related to the issue of interlimb coupling differences across tasks, is whether there are any similarities in the underlying mechanism(s) driving these relations. One suggestion is that bilateral coupling reflects changes in the amplitude of muscle activity and/or the relation between muscles (Kelso 1984; Jeka et al. 1993; Swinnen et al. 1996; Swinnen et al. 1997). For example, during isotonic movements, it has been argued that the resultant movement reflects the preference for the motor system to tightly couple muscle activity across limbs (Swinnen and Wenderoth 2004; Carson 2005). Under these conditions, coactivation is commonly reported for homologous muscles pairs (Riek and Woolley) while the pattern of activity between antagonist muscles is typically phasic or alternating (Kelso et al. 1979; Kelso and Schoner 1988). This pattern is in contrast to isometric tasks where cocontraction between relevant muscles is more typical (Carson 1995; Carson et al. 2000; Laidlaw et al. 2002; Maluf et al. 2005) and bilateral tremor tasks where low levels of muscle activity and no intermuscle coupling has been reported (Elble 1996; Koster et al. 1997; Hurtado et al. 2000; Morrison et al. 2006).

Together, it would appear that different movement outputs are characterized by differing levels of muscle activity and variations in the pattern of coupling between effectors. However, there have been few direct assessments of how different types of movements performed with the same effectors vary with regard to measures of movement variability, bilateral coupling, and muscle activity. One suggestion is that
changes in interlimb coupling across tasks are brought about by restrictions on the motor output of the effectors. Further, it may be that increases in coupling between limbs could be reflected by increased muscle activity and reduced variability of the resultant motor output. Thus, this study was designed to examine what relation exists between the variability of a given motor output, coupling dynamics and underlying neuromuscular outputs during the performance of three fundamentally different movements (e.g., postural, isometric, isotonic actions) using the same effectors. It was hypothesized that; a) bilateral coupling and muscle activity would increase while the variability of the movement outputs would decrease as the task changed from a postural tremor one to isometric and isotonic tasks, and b) increased coupling between the limbs would be reflected by increased levels of muscle activity.

### Methods

#### Participants

Twelve young adults (age: 21.9 ± 3.1 yrs) who were recruited from the University student population participated in this study. All subjects reported to be right handed, were physically active, had normal or corrected-to-normal vision, and reported no known neuromuscular, cognitive or proprioceptive deficits that could influence performance. Twelve hours before testing, participants were required to abstain from any form of stimulant that may impact on limb tremor, including moderate-high intensity exercise, alcohol and/or caffeine ingestion. Written informed consent was obtained from each subject before testing. All experimental procedures complied with the University IRB guidelines and were consistent with the Declaration of Helsinki.

#### Apparatus

For all tasks, surface electromyograms (EMGs) were collected bilaterally using bipolar Ag/AgCl EMG electrodes which were positioned over the belly of the extensor digitorum communis (EDC) and flexor digitorum superficialis (FDS) muscles of each arm. Electrodes were placed in parallel with the direction of the underlying muscle fibers with an interelectrode distance of 2 cm. EMG signals were amplified using Coulbourn isolated bioamplifiers (V75–02, sample rate 1000 Hz).

For the postural and isotonic tasks, kinematic measures of physiological tremor and voluntary finger flexion/extension actions were measured using two Coulbourn uniaxial accelerometers (V94–41, range ±10g; mass 12 g) and amplified through a Coulbourn strain gauge transducer coupler (V75–25A, sample rate 1000 Hz). Accelerometers were attached to the dorsal distal aspect of both index fingers as per our previous work (Morrison and Newell 1999; Morrison et al. 2006). These devices were positioned so the measurement axis was perpendicular to the ground during the postural task.

Isometric force was recorded using a pair of Eltran EL-500 load cells (ELFS-B1–50N). These devices recorded compressive forces produced by each finger. Force signals were amplified through a Coulbourn strain gauge transducer coupler at a sample rate of 1000 Hz. Before testing, the accelerometers and load cells were calibrated. The accelerometers were statically calibrated by using the acceleration
of gravity. A line of best fit was fitted between 0–1 g of acceleration after tilting the measurement axis of the accelerometer through 90°. The load cells were statically calibrated by loading the cell with/without a 1.25 kg weight and then applying a line of best fit between 0–12.2625 N.

**Data Collection Procedures**

Each individual performed a series of different bilateral movements using the index fingers of both arms. The specific movement tasks were; 1) a postural tremor task, 2) an isometric force task (four levels; 20% and 40% MVC, performed at a sinusoidal and constant force level) and 3) an isotonic finger tapping task (two levels; in-phase and out-of-phase). Six 30 s trials were performed for each bilateral movement task condition with the presentation being counter-balanced between participants to minimize any order effects. Before performing these bilateral tasks, measures of each person’s maximum voluntary contraction (MVC) levels were attained for each subject. During all testing (MVC and bilateral tasks), individuals were seated upright with their forearms and hands resting on a table in front of them. The height of the table was adjusted so the forearms and hands rested conformably on it. In this position, the approximate angle of the upper arm to forearm was about 90°. A 17 in. computer flat-screen monitor was also positioned on the table approximately 35 cm in front of each person. When required, individuals were given self-determined periods of rest between trials to reduce the influence of fatigue. An illustration of the relative positions of the hand and finger segments of a single arm during each movement task is shown in Figure 1.

**Isometric Force MVC Assessment.** The MVC’s were used to determine the isometric loads (20% and 40% MVC). In the seated position, the index finger of each hand was flexed to rest on the load cell (Figure 1b). Each person was required to press (flex) as forcefully as possible against both load cells using both fingers. Individuals were instructed the keep their hand and forearms on the table during all testing. This protocol consisted of three 4 s MVC contractions, with 60 s rest between trials. The greatest total force recorded in any of the three trials was considered as the MVC.

**EMG-MVC Assessment.** Measures of the maximal level of EMG activity from the EDC and FDS muscles for each arm were also collected. With the same body position as for the isometric force-MVC task, participants performed three maximal isometric finger flexion and extension actions against a fixed object (for a total of six contractions per arm). Three 4 s contractions were performed for each individual muscle and each arm. The greatest EMG levels recorded in any of the three trials was considered as the maximum value and used to normalize muscle activity across tasks. A baseline (resting) measure of EMG activity was also obtained where subjects placed both arms on the table and were instructed to completely relax their arm.

**Postural Tremor Task.** Tremor within the index fingers of both arms was assessed for all subjects while they performed a bilateral pointing task in the previously described position. With their hands and forearms resting on the table, persons were instructed to extend their index fingers (Figure 1a). The task goal was to focus on the finger tips to minimize the movement at the tip of the index finger.
For this task, each person was asked to place their fingers on the load cells (Figure 1b) and press down with the goal of matching their total force output (displayed in yellow on the computer monitor) to a target force line (displayed in red on the same monitor). The position of the hand and finger in 1c was the same as for the MVC determination. The movement goals for the postural tremor task to simply hold the finger against gravity. For the isometric task, the goal was to push on the load cell with each index finger to produce the required force levels (as displayed on a computer monitor). For the isotonic task, the goal was to produce either an alternating or in-phase flexion/extension action.

**Isometric Force Task.** For this task, each person was asked to place their fingers on the load cells (Figure 1b) and press down with the goal of matching their total force output (displayed in yellow on the computer monitor) to a target force line (displayed in red on the same monitor). The target and total force-time trajectory lines moved from left to right across the monitor. The position of each person’s forearms and hands were as previously described. The target line corresponded to 20% and 40% of the subject’s MVC. Only the total force output, which represented
the combined output from each index finger, was displayed on the computer screen. Subjects were instructed to minimize the deviation between their total force output and the red target line. Each subject performed four conditions that represented all combinations of two independent measures; mean force level (20% MVC and 40% MVC) and target shape (constant and sinusoidal). The sinusoidal target shape waveforms oscillated at 0.1 Hz with amplitude of ±5% MVC around the mean forces of 20% MVC or 40% MVC (Keogh et al. 2006). Six 30 s trials were performed for each of these four force conditions.

**Isotonic Task.** In the same seated position, each participant produced voluntary flexion/extension (tapping) action using both index fingers (see Figure 1c). Both in-phase (synchronous) and out-of-phase (alternating) finger tapping conditions were performed. Before data collection, each participant practiced the tapping actions, coordinating their movements with an auditory metronome (set at 1 Hz). Following two practice sessions, the auditory feedback was removed and each individual performed these actions at a self-selected (preferred) comfortable pace. No significant differences were observed in the frequency at which individuals performed the task. Individuals were instructed to focus on their actual finger for the duration of each trial.

**Data Analysis**

As the force data were assessed under both constant and sinusoidal conditions, the total force output was detrended before analysis so that any variability in force output would reflect that of the total and not the target force. This was done by subtracting the target force from the total force produced by each person (Newell and Slifkin 1998; Sosnoff and Newell 2006; Sosnoff et al. 2006). The accelerometer and force data were filtered using a second-order low-pass Butterworth filter with cut-off frequencies set at 40 Hz. The EMG data were rectified and band-pass filtered (10–400 Hz). All data analysis was performed using custom programs developed in Matlab version 7.0 (MathWorks).

**Frequency Analysis.** The specific measures assessed related to the frequency at which the maximum amplitude (peak power) of the acceleration/force outputs was observed (peak power frequency, PPF). Frequency analyses were performed on the filtered acceleration and force data within the range of 0–40 Hz using Welch’s averaged, modified periodogram method (512 data point Hanning window).

**Signal Regularity.** The degree of regularity of the force and accelerometer signals was assessed using Approximate Entropy (ApEn) analysis (Pincus 1991). This measure obtains the repetition of vectors of length \( m \) and \( m+1 \) that repeat within a tolerance range \( r \) of the standard deviation of the time-series. ApEn analysis measures the conditional probability of the time series signal \( X \) by providing a measure of the (logarithmic) likelihood that runs of patterns that are close for \( m \) observations remain close on the next incremental comparisons. Thus it provides an estimate of the probabilistic nature of a time series signal. The parameters set for the calculation of ApEn values \( (m = 2 \text{ and } r = .2) \) were based upon previous studies (Pincus 1991). ApEn is calculated as the natural logarithm of the ratio of the count of recurring vectors of length \( m \) against that of \( m+1 \), yielding the equation:
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$$ApEn(\bar{X}, m, r) = \ln \left[ \frac{C_m(r)}{C_{m+1}(r)} \right]$$

This analysis returns a single value for the time series signal within the range of 0–2. Higher values of ApEn represent lower repeatability of vectors of length $m$ to that of $m+1$, marking lower predictability of future data points, and greater irregularity within the time-series. Lower values represent a greater repeatability of vectors of length $m+1$, and are thus a marker of higher regularity in the time series. Increases in ApEn have been interpreted as an increase in the signal’s time domain complexity (Pincus, 1991).

**Coefficient of Variation.** An indication of the magnitude of variability for the postural tremor, isometric and isotonic outputs of each finger was determined using the coefficient of variation ($CV = SD/\text{mean}$).

**Coupling Measures**

**Cross-Correlation.** A measure of the degree of interlimb coordination was provided by cross-correlation analysis (Pearson product moment). The peak coefficient between two signals was calculated over a range of time-lags (0–5 s) with the maximal value being used as a measure of the coupling strength. The time lag at the peak was also recorded.

**Cross-ApEn.** Coupling relations were also calculated by applying Cross-ApEn to paired signal outputs (Pincus and Singer 1996; Pincus 2000). This analysis determines the degree of synchrony of two time-series normalized to unit variance. It is similar to that of ApEn, as it obtains counts of pairs of $m$ points from the two time-series ($v$ and $u$) that repeat sequentially within a tolerance range of $r$. The parameters set for the Cross ApEn calculations ($m = 2, r = .2$) were based upon previous studies (Pincus et al. 1991; Pincus 2001). Higher values of Cross-ApEn are representative of lower synchrony (greater independence) between the two time-series, while lower values represent greater synchrony and similarity (Pincus et al. 1991; Pincus 2001). The equation for Cross-ApEn is as follows;

$$\text{CrossApEn}(\bar{X}, m, r)(v \| u) = \phi^m(v \| u) - \phi^{m+1}(v \| u)$$

**Muscle Activation Measures**

**EMG Amplitude.** An indication of the degree of activity for the EDC and FDS muscles of each arm was determined by calculating the root mean square (RMS) of each EMG signal (bin size 100 ms). All EMG values were normalized to the maximal EMG values and expressed as a percentage.

**Coherence Analysis.** The nature of any intermuscle relations was assessed in the frequency domain using coherence analysis. Peak coherence measures between the two EMG signals were calculated within the range 0–400 Hz (window size 512 data points; binwidth = 0.9785 Hz). To assess whether the level of coherence between any two signals was significantly different from zero, a 95% confidence
interval was calculated according to the methods described by Halliday and colleagues (Halliday et al. 1995).

**Statistical Analysis**

To determine whether there were any differences in the measures of signal variability, EMG or coupling as a function of changes in task or limb, a repeated measures generalized linear model (GLM) was used. Where significant effects were highlighted by the GLM results, planned contrasts (one-way ANOVA's) were used to determine the specific differences between means. All statistical analyses were performed using SAS statistical software (SAS Institute Inc., NC), with the risk of Type I error set at \( p < .05 \).

**Results**

**Descriptive Data**

**Frequency Analysis.** An example of the typical signals and respective power spectral characteristics for the postural tremor, isometric force (20% MVC, sinusoidal) and isotonic flexion/extension (out-of-phase) actions is shown in Figure 2. The frequency profile of the tremor signal was broadband in appearance, with peaks being observed between 8–12 Hz (mean PPF; 9.87 Hz; SD 2.34 Hz) and 18–26 Hz (mean PPF; 22.26 Hz, SD 4.32 Hz). As expected, the frequency signal for the isotonic and isometric tasks was more visually regular, with a single dominant peak being found within a lower frequency range. For the four isometric tasks, the peak was between 0–1 Hz (mean PPF; 0.58 Hz; SD 0.24 Hz) and, for the two isotonic tasks, between 0–2 Hz (mean PPF; 1.22 Hz; SD 0.73 Hz). Consequently, a significant difference between tasks in terms of the PPF was found (left finger PPF \( F_{6,66} = 72.91 \); right finger PPF \( F_{6,66} = 21.62 \); all \( p \)'s <0.001), highlighting the significant difference for the frequency at which the peak power was found for the respective actions. For the two isotonic tasks, no difference in the PPF was observed between the in-phase and out-of-phase actions. Similarly, no significant difference in PPF was found between the four different isometric actions.

**Signal Regularity (ApEn).** A significant main effect for task was found for the outputs of both the right (\( F_{6,66} = 1443.31 \); \( p < .0001 \)) and left fingers (\( F_{6,66} = 2640.53 \); \( p < .001 \)). Planned contrasts revealed that the postural tremor task had a significantly higher ApEn values (reflecting a more variable signal) compared with the values during the isometric and isotonic tasks. A significant difference was also found between the two isotonic and the four isometric movement tasks, with ApEn scores being significantly lower under isometric conditions (all \( p \)'s<.001). No significant limb effect was observed. While significant effects were found between the different tasks, no difference in ApEn scores were found between the in-phase and out-of-phase actions, or across the four isometric conditions. Figure 3 illustrates the changes in mean ApEn and CV values for the postural tremor, isometric force and isotonic tasks.

**Coefficient of Variation.** The results revealed a significant main effect for task for the acceleration/force outputs for the right (\( F_{6,66} = 308.89 \); \( p < .0001 \)) and
Figure 2 — Representative time and frequency series outputs for the postural (tremor) task, isometric force production (20% MVC, sinusoidal) and isotonic (out-of-phase) finger tapping movements. All traces were attained from a single subject during a single trial within each condition. For the force traces, note that while the force signal for each finger are shown, these outputs were not displayed to the subject during the course of each trial.
Figure 3 — Result of the ApEn and Coefficient of Variation (CV) analysis. Both Average values are displayed for the postural finger tremor, isometric force production and isotonic movement tasks. Increased ApEn values reflect greater irregularity within the time-series while lower values reflect that the signal is more regular (less complex). Error bars represent one $SE$ of the mean. Summary values were collapsed across arms.
left fingers (F_{6,66} = 260.03; \ p < .0001). Planned contrasts revealed the degree of variability was significantly higher during the postural tremor task compared with the other movement conditions. In addition, the amount of variation observed for the force signal during the isometric tasks was significantly lower than that found during the two isotonic tasks (all p’s<.001). A significant difference was also found between the four isometric conditions with the 40% MVC tasks having significantly greater variability than the 20% MVC tasks. No limb effect was found for this measure nor were there any significant differences in the CV values between the two isotonic actions.

**Coupling Measures**

**Cross Correlation.** A significant main effect for task was found for the degree of coupling between the left and right fingers (F_{6,66} = 264.53; \ p < .001). Planned contrasts revealed that the degree of coupling was significantly lower for the postural movements compared with the remaining actions (isotonic and isometric, all p’s<.001). In addition, differences were seen between the four isometric tasks and the two isotonic tasks with the peak values being higher for the voluntary finger flexion/extension tasks. Assessment of the time lags associated with each action showed a significant difference between all three tasks (F_{6,66} = 15.56; \ p < .001). For the postural tasks, a zero time lag was found for the outputs of the left and right fingers. Under isotonic and isometric conditions, a lag of between 40–60 ms and 80–160 ms respectively was recorded between the fingers. No differences in the correlation values or time lags were observed between the two isotonic or the four isometric actions. Figure 4 illustrates the pattern of change in the peak correlation and Cross-ApEn values across the different tasks.

**Cross-ApEn.** A significant task effect for the coupling relations between the force/acceleration signals of for left and right fingers was found (F_{6,66} = 245.82; \ p < .0001). Planned contrasts showed that the highest degree of synchrony (lower Cross-ApEn) was observed during the four isometric conditions as compared with the isotonic and tremor actions. Similarly, a difference was found between the postural and isotonic movements with higher Cross-ApEn values being seen for the postural conditions (all p’s<.001). No difference in the Cross-ApEn scores between the in-phase and out-of-phase actions or the four isometric actions was observed.

**Muscle Activation Measures**

**EMG Amplitude.** Analysis of the (normalized) EMG data revealed a significant main effect for task across the four muscle groups (left FDS F_{6,66} = 107.82; left EDC F_{6,66} = 93.40; right FDS F_{6,66} = 137.57; right EDC F_{6,66} = 15.61; all p’s <0.001). Planned contrasts revealed that a higher degree of muscle activity was observed during the 40% MVC isometric tasks compared with the other movements (all p’s<.001). Under isometric conditions, the level of activation within each muscle was of the order of 10–20% MVC. The level of muscle activity was also significantly greater for the 20% MVC isometric tasks compared with the two isotonic tasks (each muscle producing between 5–8% MVC) and the postural tremor task (1–3% MVC; all p’s<.001). Similarly, activity during the isotonic task was greater than that during the tremor task.
Figure 4— Mean peak cross correlation values, the time lags associated with the peak values and Cross-ApEn scores for different postural, isometric force production and isotonic movement tasks. The Cross-ApEn values represent the degree of self-similarity in the resultant motor outputs for either finger. Higher Cross-ApEn values represent lower synchrony (greater independence) between the two signals while lower values represent greater synchrony/similarity between respective signals. Error bars represent one SE of the mean. As there was no significant limb effect for either measure, the representative values were collapsed across arms.
movements (all p’s<.001). No significant differences between limbs were observed nor were any differences observed in the RMS EMG between the in-phase and out-of-phase actions. Figure 5 illustrates the mean changes in normalized muscle activity for each arm as a function of the postural, isotonic and isometric tasks.

![Image of Figure 5](image)

**Figure 5** — Mean Normalized EMG results for each muscle group across the different task conditions. As there was no significant limb effect, the representative values were collapsed across arms. Error bars represent one SE of the mean.

**Coherence Analysis.** A significant main effect for task was observed for the maximum coherence ($F_{6,66} = 19.22; p < .001$). Post hoc analysis revealed that the coherence between all muscles was greatest under isometric conditions (range: 0.75–0.97). For isotonic actions, a moderate degree of coupling was observed between the flexor and extensor muscles of both arms (range: 0.66–0.82). For these tasks, peak coherence was observed between 20–40 Hz. Under postural conditions, there was no evidence of muscle-muscle coupling either within or across limbs (coherence <0.11).
Discussion

This study examined the relation between measures of movement variability, coupling and muscle activity during the performance of bilateral postural, isometric, and isotonic actions with the same effectors. It was predicted that the strength of the coupling relation would form a continuum with postural tremor actions exhibiting the lowest level of coupling while isotonic actions revealing a higher degree. Further, those movements characterized as having increased interlimb coupling would be associated with increased muscle activity and reduced variability of the respective movement signal. However, the results only partially support this prediction. While the strength of the coupling relations did increase from the postural tremor to isotonic actions, the changes in variability and muscle activity did not follow this same progressive pattern.

Coupling and Variability of Bilateral Movements

Although the movement signals collected for each task were different (i.e., force, acceleration), for the purposes of this discussion, all will be discussed collectively as representative of the motor output signal. Of the three types of movements performed, the one which exhibited both the highest degree of variability (highest CV values) and was the most irregular (highest ApEn) was the tremor task. The frequency profile for tremor was also more broadband, with prominent peaks between 8–12 Hz and 18–26 Hz. This association between increased variability and multiple frequency components for postural tremor is consistent with previous reports (Vaillancourt and Newell 2000; Hong et al. 2008). The tremor responses were also characterized by low levels of muscle activity across antagonist pairs (less than 5% of MVC) and no evidence of significant interlimb or muscle-muscle coupling. It has been suggested that this lack of coupling reflects that the motor output propagated to each limb is independent of that in the other limb (Marsden et al. 1969; Morrison and Newell 1999; Hwang et al. 2006) and is driven by uncoupled or parallel neural oscillators within the CNS (Bernstein 1967; Elble and Koller 1990). This bilateral independence is considered a feature of postural tremor actions since it is observed for both healthy older persons (Marsden et al. 1969; Morrison et al. 2006) and is relatively unaffected by various task constraints including increasing limb stiffness (Morrison and Newell 2000), fatigue (Morrison et al. 2005), altering body position (Hwang et al. 2006; Morrison and Sosnoff 2009), or increasing the number of upper limb segments used to perform the task (Morrison and Newell 1999). Under tremor conditions, these findings support the view that decreased coupling can be reflected by more variable movement dynamics and lower levels of muscle activity.

As predicted, the level of coupling was greatest for the isotonic tasks in comparison with the isometric and tremor actions. Strong coupling was observed for all isotonic actions, irrespective of whether it was performed in-phase or out-of-phase. Similar to tremor generation, it has been suggested that the pattern of interlimb coordination observed during isotonic actions is driven by parallel nonlinear oscillators, although here the oscillators are said to be strongly coupled (Haken et al. 1985; Krampe et al. 2000; Semjen and Ivry 2001; Assisi et al. 2005; Krampe et al. 2005). While subtle alterations in coupling have been reported as a function of manipulating factors such as the timing of each limbs action, the general trend
is to preserve strong coupling (Kelso and Jeka 1992; Jeka et al. 1993; Buchanan et al. 1997). Indeed, even under situations where subjects are instructed to move both limbs in an independent fashion or to perform a complex polyrhythmic action, the reported level of coupling between the limbs is still high (Krampe et al. 2000; Newell et al. 2000a; Newell and Vaillancourt 2001).

While coupling strength increased systematically from postural-isometric-isotonic actions, this arrangement was not reflected by a similar pattern of change in movement variability or muscle activity. Although the isotonic movements exhibited the greatest coupling, the least variable output was during the isometric force production task, irrespective of the MVC required (20% or 40%) or whether the action required sinusoidal or constant force tracking. The highest degree of muscle activity (10–20% of each muscle’s MVC) was also observed during this condition. In comparison with the tremor movements, some similarities were seen between the isotonic and isometric actions. Both were characterized by a single, low frequency component. For isometric tasks, the peak were observed around 0.5 Hz while, for the isotonic conditions, a prominent peak occurred at 1.2 Hz. The presence of singular frequency components can be associated with a less variable motor signal (Newell and Slifkin 1998; Sosnoff and Newell 2006; Sosnoff et al. 2006), an observation reflected by the lower ApEn values and lower CV for both these actions in comparison with the tremor task.

Another interesting aspect to emerge from this study was that, even though the isotonic movements exhibited a higher degree of coupling, it was actually the isometric movements that exhibited the greatest synchrony over time (lower Cross-Apen). This result is notable in that it illustrates that while the isotonic movements exhibited a higher degree of time-locking compared with the other movements, the outputs from the two fingers during the isometric task were more similar in regards to their overall pattern. What this result highlights is the examination of linear and nonlinear coupling can lead to different conclusions regarding any interlimb relations. In this respect it is essential to consider coupling indices that capture both the structural similarities between signals and those more traditional measures which evaluate the temporal coupling relations.

**Muscle Activity and Coupling**

One possibility is that any coupling changes are driven by changes in muscle activity—a suggestion which certainly has merit for the transition from an alternating action to an in-phase one during isotonic movements (Kelso 1984; Jeka et al. 1993; Swinnen et al. 1996; Swinnen et al. 1997). However, the results of the current study do not unilaterally support this position for other actions. While the lowest level of muscle activity and coherence was certainly observed during the postural tremor task, the highest degree of activity was during the isometric actions (10–20% of MVC), a movement task which only exhibited a moderate degree of interlimb coupling. Together these results highlight that the amplitude of muscle activity is not the only factor which contributes to coupling during these tasks and that other potential variables also play a role to the coupling relations that emerge. One factor which could be the degree of (augmented) feedback provided. While the visual feedback for the isotonic and postural task were similar in that the instructions were to focus on the finger motion, during the isometric task, only visual feedback relating to the total force output was provided. Given the impact visual
feedback has on these respective movement outputs (Keogh et al. 2004; Sosnoff and Newell 2005), the possibility that the form of the visual feedback may contribute to the differences seen across tasks cannot be discounted. Other variables which may influence the observed differences in coupling include the selected muscle force ranges, the possibility of differing levels of cocontraction across tasks and peripheral feedback mechanisms, which were not assessed in the current study. In general it has been shown that increased levels of muscle force can lead to increased variability of the movement, whereas increased sensory feedback reduces movement variability (Slifkin and Newell 1999; Slifkin and Newell 2000; Sosnoff and Newell 2005; Sosnoff and Newell 2006). As some of these factors were inherently different between the postural, isotonic, and isometric tasks, it is unlikely that differences in variability between tasks are solely attributed to changes in bilateral coupling strength and/or any singular change in the level of muscle activity. Rather, it may be that the specific variables which affect the movement signal vary subtly as a function of the task performed. For example, studies of postural tremor have reported that intrinsic mechanical properties of a segment such as the limb inertia can be a major contributor to the resultant tremor signal (Stiles and Randall 1967; Elble and Randall 1978; Homberg et al. 1987; Elble 2000). However, the contribution of this variable to force production tasks is negligible because of the nature of the action (Morrison and Newell 1998). Similarly, coactivation between relevant muscle groups would appear to be more commonly reported during isometric tasks (Carson 1995; Carson et al. 2000) in comparison with tremor (Keogh et al. 2004; Keogh et al. 2010) or isotonic actions (Morrison and Sosnoff 2009).

Overall, the current study highlights that, when performing different bilateral tasks with the same effectors, the pattern of change in interlimb coupling cannot wholly be explained by changes in signal variability or the level of muscle activity. While lower levels of coupling observed during postural tremor tasks are probably driven by low levels of muscle activity, for isometric and isotonic tasks, the coupling relations are not similarly reflective of increases in muscle activity and movement variability. Instead, the relation between bilateral coupling, variability and muscle activity varied across the respective actions, the task-specific differences of each movement.

References


