Load-Independent Contributions From Motor-Unit Synchronization to Human Physiological Tremor

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Halliday, David M., Bernard A. Conway, Simon F. Farmer, and Jay R. Rosenberg. Load-independent contributions from motor-unit synchronization to human physiological tremor. *J. Neurophysiol.* 82: 664–675, 1999. This study describes two load-independent rhythmic contributions from motor-unit synchronization to normal physiological tremor, which occur in the frequency ranges 1–12 Hz and 15–30 Hz. In common with previous studies, we use increased inertial loading to identify load-independent components of physiological tremor. The data consist of simultaneous recordings of tremor acceleration from the third finger, a surface electromyogram (EMG), and the discharges of pairs of single motor units from the extensor digitorum communis (EDC) muscle, collected from 13 subjects, and divided into 2 data sets: 106 records with the finger unloaded and 84 records with added mass from 5 to 40 g. Frequency domain analysis of motor-unit data from individual subjects reveals the presence of two distinct frequency bands in motor-unit synchronization, 1–12 Hz and 15–30 Hz. A novel Fourier-based population analysis demonstrates that the same two rhythmic components are present in motor-unit synchronization across both data sets. These frequency components are not related to motor-unit firing rates. The same frequency bands are present in the correlation between motor-unit activity and tremor and between surface EMG activity and tremor, despite a significant alteration in the characteristics of the tremor with increased inertial loading. A multivariate analysis demonstrates conclusively that motor-unit synchronization is the source of these contributions to normal physiological tremor. The population analysis suggests that single motor-unit discharges can predict an average of 10% of the total tremor signal in these two frequency bands. Rectified surface EMG can predict an average of 20% of the tremor; therefore within our population of recordings, the two components of motor-unit synchronization account for an average of 20% of the total tremor signal, in the frequency ranges 1–12 Hz and 15–30 Hz. Our results demonstrate that normal physiological tremor is a complex signal containing information relating to motor-unit synchronization in different frequency bands, and lead to a revised definition of normal physiological tremor during low force postural contractions, which is based on using both the tremor spectra and the correlation between motor-unit activity and tremor to characterize the load-dependent and the load-independent components of tremor. In addition, both physiological tremor and rectified EMG emerge as powerful predictors of the frequency components of motor-unit synchronization.

INTRODUCTION

The performance of maintained voluntary postural tasks in healthy humans is accompanied by small fluctuations in limb position, referred to as physiological tremor. Normal physiological tremor is a complex signal resulting from interactions between several mechanical and neural factors (Elble 1986; Elble and Koller 1990; Lakie et al. 1986; Stiles 1980; Stiles and Randall 1967). It contains different components that can be characterized by the presence of distinct frequency components in the estimated spectrum of a tremor signal (Halliday and Redfearn 1956; Stiles and Randall 1967), which have been categorized into two types. One type is due to the natural resonant frequency of the limb segment and is sensitive to inertial loading, with increased loading decreasing the resonant frequency (Randall and Stiles 1964; Robson 1959; Stiles and Randall 1967). In the case of hand extensor muscles, this mechanical resonance component has been termed the mechanical reflex component of tremor (Stiles 1980). The frequency range for this component of postural finger tremor measured about the metacarpophalangeal joint is in the range of 15–30 Hz for the unloaded finger (Stiles and Randall 1967). For tremor about the wrist and elbow joints the ranges of frequencies reported for this component of tremor are 8–12 Hz (Elble and Randall 1978; Lakie et al. 1986) and 3–5 Hz (Fox and Randall 1970), respectively. The second type of frequency component in normal physiological tremor is load independent, i.e., the frequency is unchanged by inertial loading or alterations in limb stiffness. Such load-independent tremor components have been reported in the frequency range of 8–12 Hz for postural tremor from the unrestrained finger (Halliday and Redfearn 1956; Stiles and Randall 1967), and during isometric contractions (Elble and Randall 1976). A smaller load-independent component at 30–40 Hz in unrestrained finger tremor recordings has also been reported (Amjad et al. 1994). Load-independent features of tremor are often considered to have a central neuronal origin (Elble and Koller 1990).

Irregularities in motor-unit firing provide the main source of perturbation to a limb during voluntary postural contractions. For an unrestrained limb segment, this stochastic input will excite the limb at its natural resonant frequency (Stiles and Randall 1967), generating the load-dependent component of tremor. Any other mechanical perturbation to the limb, either external or internal (i.e., arterial pressure pulse), will contribute to the magnitude of this load-dependent component of tremor.

Several different mechanisms have been proposed for the

load-independent components of physiological tremor. After examination of tremor spectra estimated from force records obtained during isometric pinch grip tasks, Allum et al. (1978) concluded that a 6- to 12-Hz peak they observed in tremor spectra resulted from the unfused twitches of late recruited motor units. This work supports the earlier view of Marshall and Walsh (1956) on tremor that normal physiological tremor reflects only motor-unit firing rates and the biomechanical properties of the musculoskeletal system (Hömberg et al. 1986). In contrast, other studies examining the relationship between motor-unit activity and tremor have proposed alternative explanations for the load-independent frequency components of tremor. Elble and Randall (1976) examined the correlation between motor-unit firing and finger tremor in force records, and between surface electromyographic (EMG) activity and force tremor. They observed a preferential amplitude modulation of extensor digitorum communis (EDC) surface EMG in the frequency range 8–12 Hz, and correlation between surface EMG and tremor, single motor-unit activity and tremor, and motor-unit pairs in the same frequency range. They attributed this to a central modulation of motor-unit firing in the frequency range 8–12 Hz, which was independent of muscle force and motor-unit firing rate. In low force contractions, Conway et al. (1995a) observed load-independent components in the correlation between single motor-unit discharges in EDC and postural finger tremor in acceleration records in the frequency bands 1–12 Hz and 15–30 Hz, which they attributed to frequency components of motor-unit synchronization. McAuley et al. (1997) observed load-independent correlations between first dorsal interosseous (1DI) EMG and tremor acceleration during index finger abduction against elastic loads at contraction strengths up to 50% maximum voluntary contraction (MVC) in three distinct frequency ranges centred at 10, 20, and 40 Hz, which they attributed to reflect rhythmic activity generated in central neural oscillators.

Pairs of motor units recorded from active muscles during maintained voluntary contractions in humans exhibit a tendency toward synchronized firing, which is thought to reflect the presence of a common presynaptic input to the motoneuron pool (Bremner et al. 1991; Buchtal and Madsen 1950; Datta and Stephens 1990; Dietz et al. 1976; Farmer et al. 1997; Milner-Brown et al. 1975). Examination in the frequency domain of motor-unit synchronization in humans has revealed distinct rhythmic components, observed as correlations over the frequency ranges 1–12 Hz and 15–30 Hz between the spike timings in motor-unit pairs recorded from 1DI, and between 1DI and second dorsal interossi (2DI) during isometric contractions (Farmer et al. 1993) and in pairs of motor units recorded from within EDC (Conway et al. 1995a) during postural contractions. Three previous studies, employing time domain measures, have investigated the relationship between the level of motor-unit synchronization and normal physiological tremor. Two studies in first dorsal interosseous (1DI) found no significant relationship between motor-unit synchronization and the peak-to-peak magnitude (Dietz et al. 1976) or root-mean-square (RMS) magnitude (Semmler and Nordstrom 1995, 1998) of tremor in force records. Similarly, Logigian et al. (1988) concluded that there was no relationship between motor-unit synchronization in the wrist extensor muscles and the RMS value of normal physiological wrist tremor. These studies have led to the consensus view that, under normal conditions, motor-unit synchronization does not contribute to physiological tremor (Allum et al. 1978; Dietz et al. 1976; Freund 1983; Logigian et al. 1988; Semmler and Nordstrom 1995, 1998). In contrast, the recent observations on the rhythmic nature of processes generating motor-unit synchronization during weak contractions (Farmer et al. 1993) and the correspondence between the frequency bands associated with motor-unit synchronization and the 1- to 12-Hz and 15- to 30-Hz load-independent components of physiological tremor (Conway et al. 1995a) suggest that the role of motor-unit synchronization in physiological tremor should be reassessed.

The present study therefore investigates the relationship between the two frequency bands present in motor-unit synchronization (1–12 Hz and 15–30 Hz) and normal physiological tremor. Our aims are 1) to clarify the role of motor-unit firing rate in the generation of physiological tremor, 2) to assess whether there is any relationship between the rhythmic components of motor-unit synchronization and physiological tremor, 3) to investigate whether this relationship exhibits any load dependency, and 4) to determine whether similar information is available using EMG instead of single motor-unit discharges, and in particular if surface EMG can predict the rhythmic components in motor-unit synchronization resulting from rhythmic inputs to motoneuron pool during maintained voluntary contractions (Farmer et al. 1993).

To distinguish between load-dependent and load-independent components of tremor, the complete data are subdivided into two sets: records obtained without additional inertial loading, and records obtained with increased inertial loading. We apply a novel Fourier-based population analysis (Amjad et al. 1997) to characterize the correlation structure across all records in each data set. The results, which are similar to those obtained by analysis of sequential records from an individual subject (Conway et al. 1995a), demonstrate that normal physiological tremor is a complex signal containing information relating to motor-unit synchronization in two distinct frequency bands.

Preliminary accounts of the present results are published in Conway et al. (1994) and Conway et al. (1995a).

METHODS

Subjects and recording procedures

Simultaneous recordings of third finger tremor, pairs of motor-unit spike trains, and a surface electromyogram (EMG) from EDC were made from 13 healthy adult subjects (12 male, 1 female, age range 22–60 yr), with informed consent from each subject and local ethical committee approval (West ethical committee, Greater Glasgow Health Board). The tremor signal was derived from an accelerometer fixed to the distal phalanx of the unsupported middle finger, while the subject was seated with the forearm pronated and the other fingers, wrist, and forearm supported and immobilized by a custom-designed rigid polypropylene cast. Two single motor units were recorded from a pair of concentric needle electrodes (Medelec DFC25) inserted into the middle finger portion of the EDC muscle. The bipolar surface EMG signal was obtained from a pair of Ag/AgCl electrodes placed ~20 mm apart on either side of the needles.

The accelerometer output was amplified and fed to a data collection interface for digitizing. The bandwidth of this signal is determined by the characteristics of the accelerometer (Entran EGAX-5), which has a flat frequency response from DC to above 200 Hz. The surface EMG signal was filtered (3–500 Hz), and amplified (×1,000) before digi-

tizing. The needle electrode signals were amplified and band-pass filtered before being passed through window discrimination devices; the transistor-transistor logic (TTL) pulses output from these were fed to the digital input of the data collection device.

Acceleration and surface EMG signals were sampled at 1-ms intervals, and motor-unit spike times were recorded with a 1-ms sampling interval.

Experimental protocol

During data collection the subject was asked to extend and maintain the middle finger in a horizontal position. The positions of the two needle electrodes were adjusted to obtain stable recordings from separate repetitively firing motor units. Single motor units were identified by their spike shape, which was continually monitored on a digital storage oscilloscope. Once stable pairs of motor units were obtained, successive records were collected, initially with the finger unloaded, then subsequently with small weights attached to the distal end of the finger. The weights were added in 5-g increments, ranging from 5 to 40 g. The addition of weights was continued until stable recordings were no longer possible from the identified motor-unit pair, either through contamination from newly recruited units or the cessation of repetitive firing.

We have used small incremental changes in limb inertia; Randall and Stiles (1964) demonstrated that 5-g increments were sufficient to alter the frequency of the 15–30 Hz load-dependent component of physiological tremor. Stiles and Randall (1967) demonstrated systematic changes in the tremor characteristics with incremental loading using 5-g increments. In addition using small incremental loading allows recordings to be made from the earliest recruited fatigue-resistant motor units.

Analytic methods

As a consequence of different conduction delays in nerve and muscle, the peak in the time domain correlation between motor-unit pairs was not always centered at zero lag. The range of peak latencies for individual records is taken to reflect these conduction delays, and delays due to interelectrode spacing (Bremner et al. 1991; Kakuda et al. 1992). Before frequency domain analysis, we corrected for these delays using a temporal alignment procedure, in which the timings of one spike train of each pair were adjusted by a constant time offset, which was chosen such that the resultant peak in the time domain correlation between each pair of spike trains was centered at zero lag. The offset was an integer multiple of the sampling interval, and varied between 0 and 9 ms. In their study of motor-unit pairs recorded from within intrinsic (1st, 2nd, and 4th dorsal interossei) and extrinsic (extensor pollicis brevis, extensor digitorum, and flexor digitorum) hand muscles, Bremner et al. (1991) obtained a range of 0–8 ms for the peak offset.

The framework and notation for the analysis of individual records is that set out in Halliday et al. (1995b). The acceleration signal, denoted by x, and full-wave rectified EMG, denoted by y, are assumed to be realizations of stationary zero mean time series. The two motor-unit spike trains, *motor unit 0* and *motor unit 1*, are assumed to be realizations of stationary stochastic point processes, and are denoted by N_0 and N_1, respectively (Conway et al. 1993). All four processes are assumed to satisfy a mixing condition, whereby sample values widely separated in time are independent (Brillinger 1981). Autospectra of these four signals are denoted by $f_{xx}(\lambda)$, $f_{yy}(\lambda)$, $f_{00}(\lambda)$, and $f_{11}(\lambda)$, respectively, an estimate is identified by the inclusion of the ^ symbol, e.g., $\hat{f}_{xx}(\lambda)$. In the frequency domain, the correlation between two processes is assessed through the use of coherence functions (Brillinger 1981; Halliday et al. 1995b; Rosenberg et al. 1989). The estimated coherence function between the two motor units is denoted by $|\hat{R}_{10}(\lambda)|^2$. Other pairwise interactions we consider are between motor units and tremor, $|\hat{R}_{x0}(\lambda)|^2$ and $|\hat{R}_{x1}(\lambda)|^2$, and between

rectified EMG and tremor, $|\hat{R}_{xy}(\lambda)|^2$ (Halliday et al. 1995b). Motor-unit synchronization has traditionally been studied in the time domain (e.g., Bremner et al. 1991). In the present study, correlation between *motor unit 0* and *motor unit 1* is assessed in the time domain through the use of a second-order cumulant density function, the estimate of which is denoted by $\hat{q}_{10}(u)$. Cumulant densities provide a general measure of statistical dependence between random processes and will assume the value zero if the processes are independent (Halliday et al. 1995b). Complete details of the analytic framework, including estimation techniques, procedures for construction of confidence limits, and a detailed analysis of a single record drawn from the present data are given in Halliday et al. (1995b).

In assessing the average strength of the four pairwise interactions within each population of recordings, we use the novel population analysis technique of pooled coherence (Amjad et al. 1997). This provides a single measure that summarizes the correlation structure across all data sets in a population. The use of pooled coherence overcomes the problems associated with the more usual examination and presentation of individual records, which may be misleading, by characterizing features that are not representative of the larger population (Fetz 1992).

Coherence and pooled coherence functions provide normative measures of linear association on a scale from 0 to 1 (Amjad et al. 1997; Brillinger 1981; Halliday et al. 1995b; Rosenberg et al. 1989). We can therefore interpret the appropriate coherence and pooled coherence estimates as providing an estimate of the contribution from motor-unit or surface EMG activity to the tremor signal. This provides a measure of the percentage of the tremor signal, at each frequency, which can be accounted for by motor-unit or surface EMG signals, allowing us to quantify frequency components of normal physiological tremor related to rhythmic neural activity, both for individual records and complete populations.

In this study we also use estimates of first-order partial coherence functions to assess whether a third process (or predictor) accounts for the relationship between two other processes (Halliday et al. 1995b; Rosenberg et al. 1989, 1998). In situations where three processes exhibit significant pairwise coherence estimates over the same range of frequencies, first-order partial coherence estimates can be used to test the hypothesis that common frequency components are involved in all of the pairwise correlations (Halliday et al. 1995b; Rosenberg et al. 1989). For the present data we examine the first-order partial coherence between the two motor units using the tremor or the rectified EMG as the predictor. The partial coherence between the two motor units using the tremor as predictor is denoted by $|R_{10/x}(\lambda)|^2$; with EMG as predictor it is denoted by $|R_{10/y}(\lambda)|^2$. If motor-unit synchronization contributes to physiological tremor, then the tremor signal, x, will be able to predict the components of $|R_{10}(\lambda)|^2$. In this case the estimated partial coherence, $|\hat{R}_{10/x}(\lambda)|^2$, will show a clear reduction in magnitude when compared with the ordinary coherence estimate between the motor units, $|\hat{R}_{10}(\lambda)|^2$, at the frequency components where motor-unit synchronization contributes to physiological tremor. Similar comments apply for interpreting the estimated partial coherence with EMG as predictor, $|\hat{R}_{10/y}(\lambda)|^2$.

RESULTS

Summary of the data sets

The present results are based on a total of 190 records obtained from 101 motor-unit pairs during 21 experiments performed on 13 subjects. The recordings were made from the earliest recruited, fatigue-resistant motor units displaying repetitive firing. For the present analysis these records were split into two data sets. The first data set, *data set one,* consists of 106 records obtained with the middle finger unloaded. The second, *data set two,* consists of the remaining 84 records

obtained with the finger loaded. The average duration for the 190 records was 89 s (range, 20–180 s).

The mean discharge rate for the 212 motor units in *data set one* was 11.9 spikes/s (range, 7.5–18.8 spikes/s), the mean coefficient of variation (c.o.v.) was 0.31 (range, 0.11–0.75). The corresponding 106 acceleration records had an average RMS value of 6.1 cm/s^2 (range, 1.1–37.0 cm/s^2).

The mean discharge rate for the 168 motor units in *data set two* was 12.4 spikes/s (range, 6.3–18.2 spikes/s), the mean c.o.v. was 0.32 (range, 0.12–0.85). The corresponding 84 acceleration records had an average RMS value of 8.1 cm/s^2 (range, 1.9–34.1 cm/s^2). The average load was 11.6 g (range, 5–40 g). The number of records at each load was 5 g, 30 records; 10 g, 26 records; 15 g, 13 records; 20 g, 8 records; 25 g, 3 records; 30 g, 2 records; 35 g, 1 record; and 40 g, 1 record.

Figure 1 illustrates a 3-s segment of data from one subject, along with estimates of the autospectra of the four signals, for one record of duration 100 s from this subject, with the finger unloaded. Log plots of the point process spectral estimates for the two motor units, $\hat{f}_{00}(\lambda)$ and $\hat{f}_{11}(\lambda)$, are shown in Fig. 1, *B* and *C*, along with the asymptotic value for a random discharge with the same mean rates and upper and lower 95% confidence limits (see Halliday et al. 1995b). The dominant feature in each estimate is a single spectral peak, at 12.6 Hz for *motor unit 0* and ~10 Hz for *motor unit 1*, these represent the mean rate of discharge of the motor units (12.6 spikes/s and 9.9 spikes/s) and illustrate that the periodic firing of each motor unit is the dominant rhythmic component identifiable in each spectral estimate. *Motor unit 0* has a more regular discharge (c.o.v. 0.18) than *motor unit 1* (c.o.v. 0.27), resulting in a more clearly defined spectral peak and a small harmonic component around 25 Hz in Fig. 1*B*. Log plots of the time series spectral estimates of the acceleration record, $\hat{f}_{xx}(\lambda)$, and the rectified EMG, $\hat{f}_{yy}(\lambda)$ are illustrated in Fig. 1, *D* and *E*. The 95% confidence interval for these estimates is indicated by the solid vertical line in the *top right* of each graph, these lines provide a scale bar against which to assess the significance of local fluctuations. The tremor spectrum (Fig. 1*D*) contains three distinct frequency bands. The dominant mechanical resonance component is centered around 20 Hz; smaller neurogenic components around 12 and 30 Hz are visible (Amjad et al. 1994; Stiles and Randall 1967). The rectified EMG spectrum (Fig. 1*E*) has two dominant peaks around 12 and 20–30 Hz, which we interpret to reflect increased power due to preferential grouping of motor-unit activity (i.e., motor-unit synchronization) in these two frequency ranges (Halliday et al. 1995b).

Pooled coherence and cumulant estimates as population measures of motor-unit synchronization

Figure 2 shows the estimated coherence $|\hat{R}_{10}(\lambda)|^2$, and cumulant density, $\hat{q}_{10}(u)$, between three individual motor-unit pairs drawn from *data set one* (unloaded). These examples, which all have the same record duration of 100 s and are taken from different subjects, illustrate the range of strengths of motor-unit synchronization and intersubject variability present within this data set. The first example (Fig. 2, *A* and *B*), estimated from the same data as illustrated in Fig. 1, has the strongest coupling, with significant coherence in two distinct frequency bands, and an estimated cumulant with a clearly
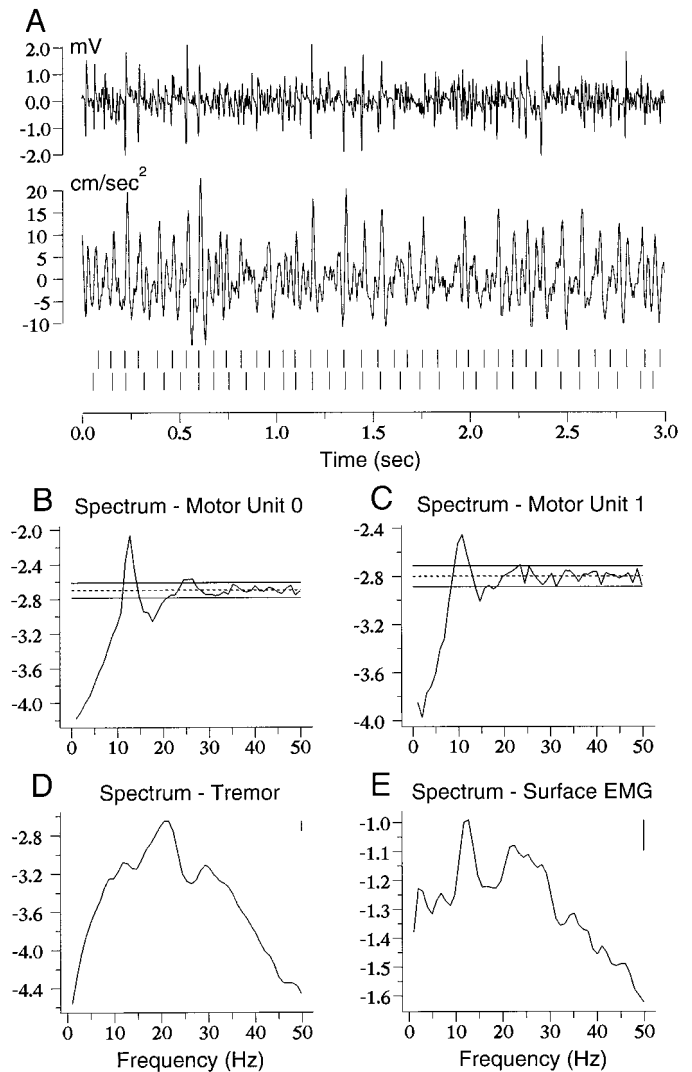

FIG. 1. Tremor, motor-unit, and electromyographic (EMG) data. *A*: a 3-s segment of data from 1 subject, illustrating raw surface EMG (*top*), the tremor acceleration signal (*middle*) and the times of occurrence of motor-unit spikes shown as vertical lines (*bottom*). Log plots of estimated auto spectra of (*B*) *motor unit 0*, $\hat{f}_{00}(\lambda)$, and *C*, *motor unit 1*, $\hat{f}_{11}(\lambda)$. Dashed horizontal lines represent the asymptotic value of each estimate; solid horizontal lines represent the upper and lower 95% confidence limits. Log plots of estimated auto spectra of (*D*) tremor signal, $\hat{f}_{xx}(\lambda)$, and (E) rectified surface EMG signal, $\hat{f}_{yy}(\lambda)$. Solid vertical lines at the top right represent the 95% confidence interval for each estimate.

defined central peak. The other two examples illustrate progressively weaker correlation, seen as a reduced magnitude in coherence estimates, and less distinct central peaks in cumulant estimates; a similar range and variation in the strength of motor-unit synchronization is present in *data set two* (not shown). We can use pooled coherence analysis to summarize the correlation structure across all 106 records in *data set one* and across all 84 records in *data set two*. These pooled coherence estimates are illustrated in Fig. 3, *A* and *B*, respectively. This population analysis across all available data results in the same correlation structure as observed for individual records, namely significant coherence in the two frequency bands, 1–12 Hz and 15–30 Hz. This result is in agreement with that of Farmer et al. (1993), who studied motor-unit synchronization in human 1DI and 2DI muscles during isometric contractions.
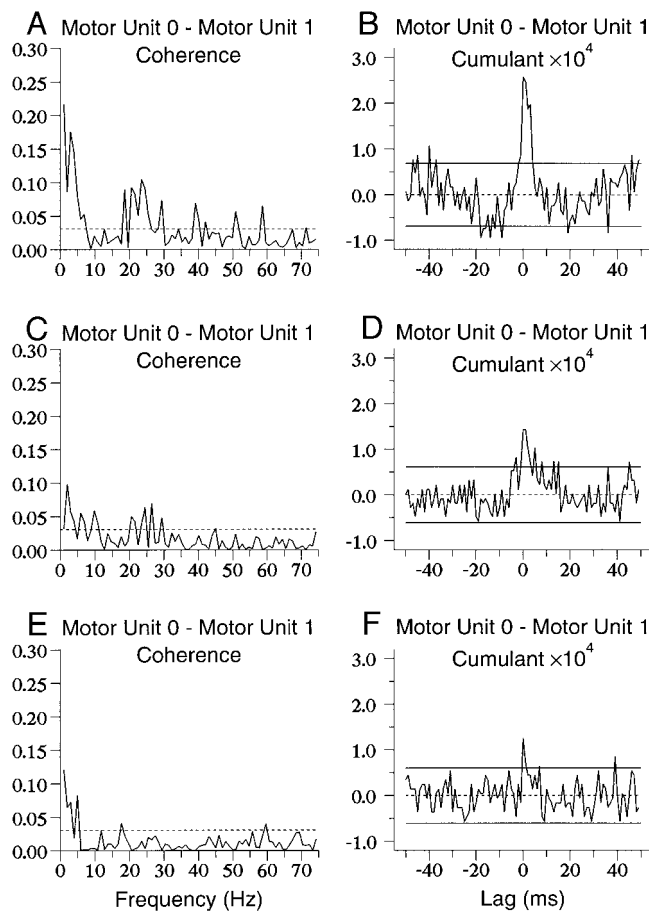
FIG. 2. Examples of motor-unit synchronization. *A, C,* and *E*: estimated coherence between *motor unit 0* and *motor unit 1,* $|\hat{R}_{10}(\lambda)|^2$, for 3 pairs of motor units recorded from extensor digitorum communis (EDC). *B, D,* and *F*: corresponding estimated cumulant densities, $\hat{q}_{10}(u)$, for the same 3 motor-unit pairs. Horizontal dashed lines in the coherence estimates (*A, C,* and *E*) and horizontal solid lines in the cumulant density estimates (*B, D,* and *F*) represent estimates of 95% confidence limits based on the assumption of independence.

In their study of motor-unit coupling Farmer et al. (1993) used a histogram to represent the proportion of motor-unit pairs with significant coherence in individual estimates at each frequency. Similarly constructed histograms are shown in Fig. 3*C* for *data set one,* and Fig. 3*D* for *data set two,* showing the proportion of coherence estimates with values above the 95% confidence limit (based on the assumption of independence and represented by the horizontal dashed line in Fig. 2, *A, C,* and *E*), at each frequency. These histograms indicate the presence of two distinct frequency bands corresponding to the peaks in the pooled coherence estimates. Pooled coherence has the advantage of further providing a measure of the strength of coupling at each frequency.

Figure 3, *E* and *F,* illustrates the corresponding pooled cumulant density estimate and confidence limits for *data sets one* and *two,* respectively; the binwidth is 1 ms. These estimates have a well-defined time course, with a central peak of around 14 ms in width. Histograms counting the proportion of individual cumulant density estimates with values above the upper 95% confidence limit (top solid line in Fig. 2, *B, D,* and *F*) in each bin, are shown in Fig. 3*G* for *data set one,* and Fig. 3*H* for *data set two.* These histograms indicate that, after the temporal alignment process, over 95% of the individual cumu-

lant density estimates in each data set have a significant peak at zero lag, indicating a high prevalence of synchronization in both data sets. In their study of motor-unit synchronization in EDC, dorsal and palmer interossei, and flexor digitorum superficialis Bremner et al. (1991) observed significant peaks in 88% of records.

Pooled coherence estimates for motor unit to tremor correlations and surface EMG to tremor correlations

Pooled coherence estimates were constructed between each motor unit and the tremor, and between the surface EMG and tremor for *data sets one* and *two,* providing a measure of the
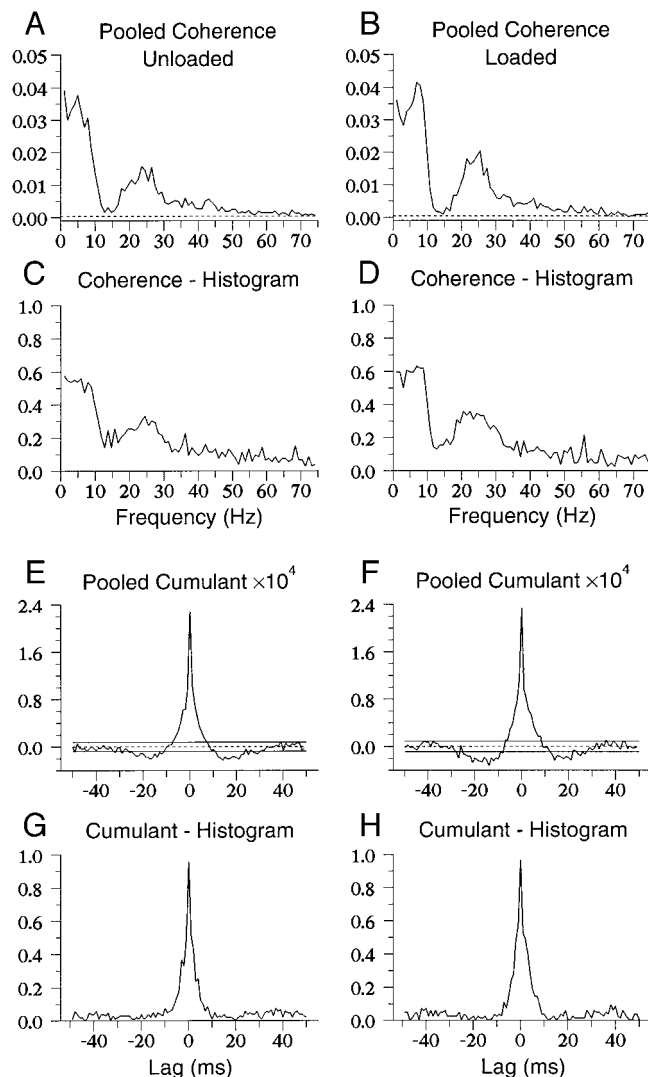
FIG. 3. Population motor-unit synchronization in *data sets 1* (Unloaded) and *2* (Loaded). Pooled coherence estimates for (*A*) all 106 motor-unit pairs in *data set 1,* and (*B*) all 84 motor-unit pairs in *data set 2.* Histograms showing fraction of individual coherence estimates that exhibit significant values above a 95% confidence limit at each frequency for (*C*) *data set 1,* and (*D*) *data set 2.* Pooled cumulant density estimates for (*E*) all 106 motor-unit pairs in *data set 1,* and (*F*) all 84 motor-unit pairs in *data set 2.* Histograms showing fraction of individual cumulant density estimates that exhibit significant values above an upper 95% confidence limit at each lag for (*G*) *data set 1* and (*H*) *data set 2.* Horizontal dashed lines in the coherence estimates (*A* and *B*) and horizontal solid lines in the cumulant density estimates (*E* and *F*) represent estimates of 95% confidence limits based on the assumption of independence.

FIG. 4. Pooled coherence estimates for *data set 1* (Unloaded). Pooled coherence estimates for all 106 records in data set one. *A*: estimate between *motor unit 0 and 1,* $|\hat{R}_{10}(\lambda)|^2$, (*B*) between *motor unit 0* and tremor, $|\hat{R}_{x0}(\lambda)|^2$, (*C*) between *motor unit 1* and tremor, $|\hat{R}_{x1}(\lambda)|^2$, and (*D*) between rectified surface EMG and tremor, $|\hat{R}_{xy}(\lambda)|^2$. Horizontal dashed lines represent estimates of the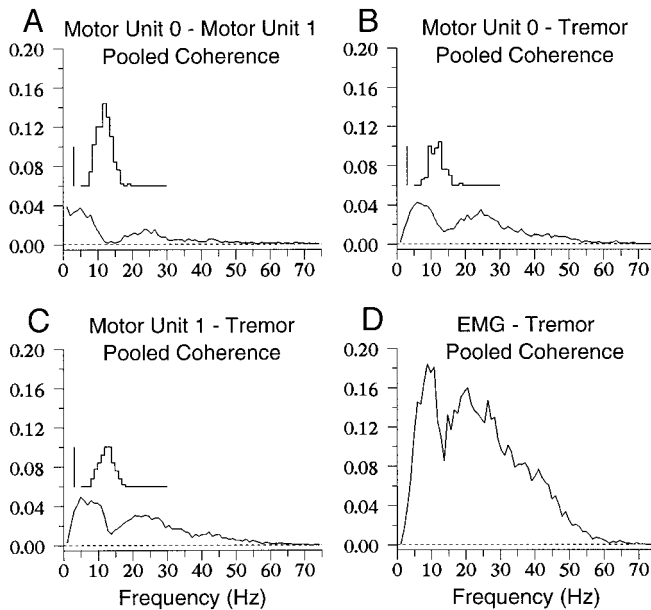 95% confidence limits based on the assumption of independence. *Insets* above the coherence estimates in *A–C* are histograms of the mean firing rates of the motor-unit discharges. Vertical scale bar to the left of each histogram represents 20 counts. Horizontal axes on the pooled coherence estimates represent the Fourier frequencies for the spectral analysis. We plot these frequencies in cycles/s (Hz); the values can also be used to indicate the mean firing rate for the histograms, in spikes/s. Histograms were constructed with a binwidth of 1 spike/s. In *A* the histogram is for all 212 motor-unit discharges; in *B* it is for the 106 discharges of *motor unit 0,* and in *C* it is for the 106 discharges of *motor unit 1.*

average contribution to the tremor from motor-unit and surface EMG activity in each data set. In accordance with the assumption of independent experiments (Amjad et al. 1997), the motor unit to tremor interactions are considered separately (because the tremor signal is common to each motor-unit pair). The choice of label (*0* or *1*) for each motor unit was specified by the channel on which it was recorded. Including the pooled motor-unit coherence estimates illustrated in Fig. 3, four pooled coherence estimates are used to characterize the interaction between motor units, EMG, and tremor. All four estimates for *data set one* are shown in Fig. 4. Histograms of the mean firing rates of the motor-unit discharges are shown above the coherence estimates in Fig. 4, *A–C.* The histogram in Fig. 4*A* is for all 212 motor-unit discharges. Those in Fig. 4, *B* and *C* are for the 106 discharges designated as *motor unit 0* and *motor unit 1,* respectively. The corresponding pooled coherence estimates and firing rate histograms for *data set two* are shown in Fig. 5.

Several points emerge from this population analysis of motor-unit pairs, surface EMG, and tremor. The first point is the similarity between the frequency bands present in these pooled coherence estimates, taken across subjects, and those present in single records from individual subjects (see also Amjad et al. 1997, Figs. 2, 5, 7, and 8; Conway et al. 1995a, Fig. 1; Halliday et al. 1995b, Fig. 4). A characteristic feature of the four pooled coherences for both data sets is the presence of the same two distinct frequency bands, 1–12 Hz and 15–30 Hz, in each estimate. The correlation between single motor units and

tremor therefore occurs at the same frequencies as the correlation between motor-unit pairs (Conway et al. 1995a). Within each data set, the peak in the superimposed firing rate histograms lies largely between these two frequency bands, thus these frequencies do not in general correspond to the firing rate of the motor units (Conway et al. 1995a). For both data sets, the pooled coherence estimate between surface EMG and tremor (Figs. 4*D* and 5*D*) is greater in magnitude than those for the motor unit to tremor estimates (Fig. 4, *B* and *C* and Fig. 5, *B* and *C*), which in turn are greater than the motor-unit coherences (Figs. 4*A* and 5*A*). The rectified surface EMG emerges as a powerful predictor of that motor-unit activity that is correlated with the tremor signal (Figs. 4*D* and 5*D*). The pooled coherence estimates between single motor-unit discharges and tremor have a peak magnitude of between 0.04–0.1 (Figs. 4, *B* and *C,* and 5, *B* and *C*), which indicates that, on average, a single motor-unit discharge can account for between 4 and 10% of the tremor signal in the two frequency bands 1–12 Hz and 15–30 Hz. The rectified EMG, which samples the activity across a number of active motor units, can account for 20% of the tremor signal in the two frequency bands 1–12 Hz and 15–30 Hz (Figs. 4*D* and 5*D*).

The presence of the same two frequency bands in the above pooled coherence estimates for both loaded and unloaded data sets, despite the increased inertial loading associated with *data set two,* implies that these two frequency bands represent load-independent contributions to tremor. To establish that
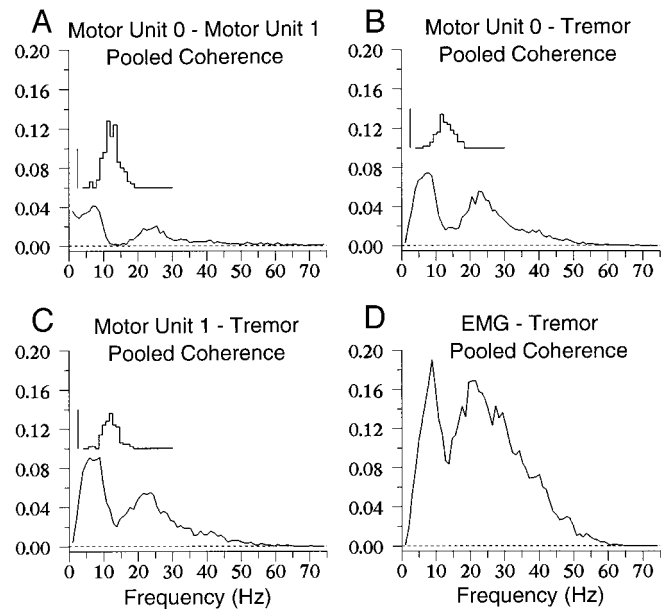
FIG. 5. Pooled coherence estimates for *data set 2* (Loaded). Pooled coherence estimates for all 84 records in *data set 2.* *A*: estimate between *motor unit 0 and 1,* $|\hat{R}_{10}(\lambda)|^2$, (*B*) between *motor unit 0* and tremor, $|\hat{R}_{x0}(\lambda)|^2$, (*C*) between *motor unit 1* and tremor, $|\hat{R}_{x1}(\lambda)|^2$, and (*D*) between rectified surface EMG and tremor, $|\hat{R}_{xy}(\lambda)|^2$. Horizontal dashed lines represent estimates of the 95% confidence limits based on the assumption of independence. *Insets* above the coherence estimates in *A–C* are histograms of the mean firing rates of the motor-unit discharges. Vertical scale bar to the left of each histogram represents 20 counts. Horizontal axes on the pooled coherence estimates represents the Fourier frequencies for the spectral analysis. We plot these frequencies in cycles/s (Hz), the values can also be used to indicate the mean firing rate for the histograms, in spikes/s. Histograms were constructed with a binwidth of 1 spike/s. In *A* the histogram is for all 168 motor-unit discharges; in *B* it is for the 84 discharges of *motor unit 0,* and in *C* it is for the 84 discharges of *motor unit 1.*

FIG. 6.   Pooled tremor and EMG spectra for *data sets 1* (Unloaded) and *2* (Loaded). *A*: log plots of estimated pooled tremor spectra, $\hat{f}_{xx}(\lambda)$, for all 106 records in *data set 1* (sol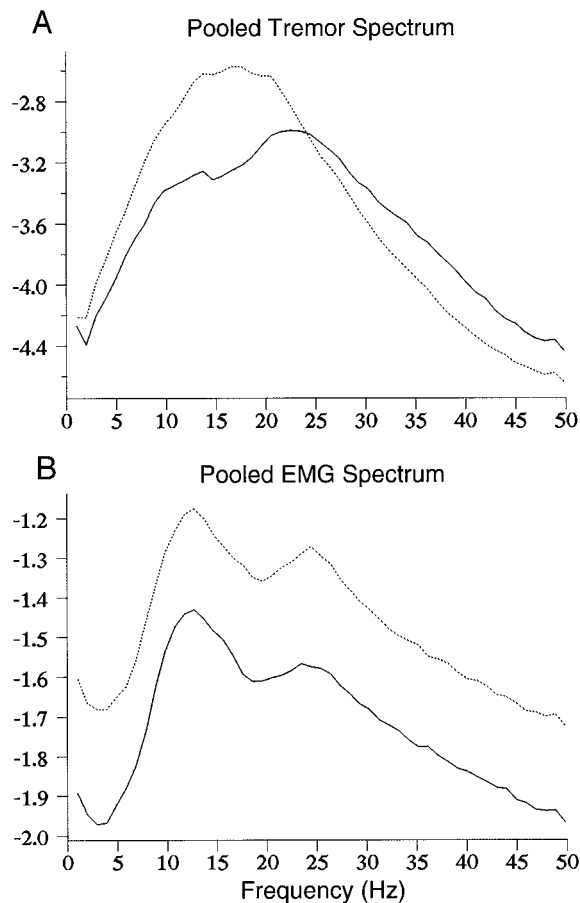id line) and for all 84 records in *data set 2* (dotted line). To obtain these pooled spectral estimates in each data set, which are representative of the frequency components across all the records, each tremor record was scaled to have the same root-mean-square (RMS) tremor value as the mean in each data set (6.1 and 8.1 cm/s^2). *B*: log plots of estimated pooled EMG spectra, $\hat{f}_{yy}(\lambda)$, for all 106 records in data set 1 (solid line) and for all 84 records in *data set 2* (dotted line), estimated as in *A* by standardizing the variance in all records across each data set.

these frequency bands reflect load independent features of the data, it has to be established that the increased inertial loading in *data set two* produced a significant alteration in the tremor characteristics as predicted by the model for the relationship between added mass, *m,* and the frequency, ω, of the dominant mechanical resonance component of finger tremor: $\omega \propto 1/\sqrt{m}$ (Stiles and Randall 1967). The average mass applied in the 84 records was 11.6 g (range, 5–40 g). The mean RMS value of the tremor increased from 6.1 cm/s^2 in *data set one,* to 8.1 cm/s^2 in *data set two*. The RMS values do not give any indication of the dominant frequency components in the tremor records. The estimated pooled spectra for each data set can be used to determine whether the frequency components in the tremor across each population have been altered by the increased inertial loading. Because the range of RMS values for individual tremor records was 1.1–37 cm/s^2, each tremor signal was scaled to have the same RMS value across each data set, 6.1 or 8.1 cm/s^2; otherwise the pooled tremor spectra would be dominated by the records with the largest RMS tremor. Figure 6 illustrates estimates of these pooled tremor spectra for each data set. The frequency of the dominant peak decreases from

23 to 17 Hz with inertial loading, which is comparable with that reported for individual subjects (Stiles and Randall 1967, Figs. 3 and 4). This alteration in the mechanical resonance component of tremor in the unsupported finger establishes the load independence of the distinct peaks in the pooled coherences illustrated in Figs. 4 and 5. The pooled EMG spectra for each data set (calculated by same approach of standardizing the variance across each data set) are illustrated in Fig. 6*B*. These have the same form as that for a single subject (Fig. 1*E*), with power concentrated around 12 and 25 Hz, which we interpret to reflect frequency components due to motor-unit synchronization across the two populations of data.

Load-independent contributions from motor-unit synchronization to physiological tremor; partial coherence analysis using tremor, and surface EMG as predictors of motor-unit synchronization

The above observations that motor-unit to motor-unit coherences and motor-unit to tremor coherences occur in the same frequency bands suggests that the processes responsible for motor-unit synchronization are transmitted to the muscle as a tension or length change and consequently may be observed as a component of the tremor signal. This can be directly tested through the application of partial coherences, in which the tremor signal is used as a predictor of the motor-unit correlation. If the tremor signal contains frequency components due to motor-unit synchronization, then the partial coherence between motor-unit pairs, with the tremor signal as predictor, will not be significant over the range of frequencies associated with the two components of motor-unit synchronization.

The EMG to tremor coherences, which also involve the same two load-independent frequency bands, suggest that surface EMG can be used as a predictor of motor-unit correlation, in which case the pooled partial coherence between the motor-unit pairs using the surface EMG as predictor will not be significant over the two frequency bands associated with motor-unit correlation.

For *data set one,* the estimated pooled partial coherence with the tremor as predictor, $|\hat{R}_{10/x}(\lambda)|^2$, is shown in Fig. 7*A*. The estimate with rectified EMG as predictor, $|\hat{R}_{10/y}(\lambda)|^2$, is shown in Fig. 7*B*. The corresponding estimates for *data set two* are shown in Fig. 7, *C* and *D,* respectively. In each graph the original estimate of pooled motor-unit coherence, $|\hat{R}_{10}(\lambda)|^2$, is shown as a dotted line, this allows a direct comparison of the pooled partial coherence with the pooled ordinary coherence.

Considering first the 15- to 30-Hz frequency band with the tremor as predictor, the partial coherence estimates (Fig. 7, *A* and *C,* solid lines) exhibit no consistent significant features in this frequency range. Therefore all frequency components in the 15- to 30-Hz frequency range present in the motor-unit synchronization are transmitted to the tremor signal, allowing it to accurately predict the motor-unit synchronization in this frequency range. We can therefore conclude that there is a significant contribution to physiological tremor resulting from motor-unit synchronization in this frequency range. Although a similar conclusion can be drawn for the 1- to 12-Hz component, the effect is more complex. The pooled partial coherence estimates (—) exhibit only a part reduction in magnitude of the significant features present in the original pooled coherence estimates (· · ·). A partial reduction can occur for two reasons:
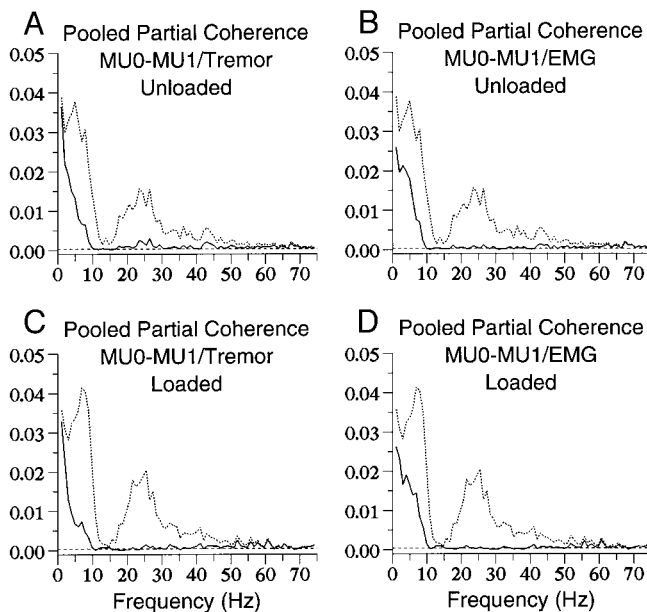
FIG. 7. Pooled partial coherence estimates for *data sets 1* and *2*. Pooled partial coherence estimates using the tremor as predictor, $|\hat{R}_{10/x}(\lambda)|^2$, (A) for all 106 records in *data set 1*, and (C) all 84 records in *data set 2*. Pooled partial coherence estimates using the rectified surface EMG as predictor, $|\hat{R}_{10/y}(\lambda)|^2$, (B) for all 106 records in *data set 1*, and (D) all 84 records in *data set 2*. Also shown as a dotted trace in each graph is the original pooled coherence estimate between the motor-unit pairs, $|\hat{R}_{10}(\lambda)|^2$. For A and B this is for the 106 motor-unit pairs in *data set 1* and is copied from Fig. 3A, and in C and D it is for the 84 motor-unit pairs in *data set 2* and is copied from Fig. 3B. Horizontal dashed lines represent estimates of the 95% confidence limits based on the assumption of independence.

1) the 1- to 12-Hz component of motor-unit synchronization does not contribute as strongly to physiological tremor as the 15- to 30-Hz component, or *2*) the contribution may involve linear and nonlinear interactions, possibly reflecting different mechanisms. Partial coherence functions are based on the assumption of linearity and cannot detect a nonlinear interaction (Halliday et al. 1995b; Rosenberg et al. 1989, 1998). On the basis of the present analysis, we cannot distinguish between either of these mechanisms. The partial reduction in the range 1–12 Hz does, however, indicate that there is a component of physiological tremor in the range 1–12 Hz, which can be attributed to this lower frequency component of motor-unit synchronization. With the exception of a small residual component in the pooled partial coherence around 22–28 Hz in *data set one* (Fig. 7A, —), comparison of this analysis for *data set one* and *data set two* reveals identical results. Therefore contributions over a similar frequency range are made to physiological tremor in both the unloaded (*data set 1*) and loaded (*data set 2*) populations. This reduction in the partial coherence estimates compared with the ordinary coherence estimates in Fig. 7, A and C, indicates that common frequency components are involved in the population correlations and establishes the rhythmic components of motor-unit synchronization as the source of the 1- to 12-Hz and 15- to 30-Hz contributions from motor-unit activity to the tremor.

The pooled partial coherence estimates using the rectified surface EMG as predictor (Fig. 7, B and D) are similar to those using the tremor signal (Fig. 7, A and C). Therefore the rectified surface EMG is as efficient a predictor of motor-unit synchronization as the tremor signal.

DISCUSSION

Relationship between physiological tremor and motor-unit activity

This study considers the relationship between physiological tremor and motor-unit activity in a number of recordings taken across subjects performing the same postural task under two conditions (unloaded and loaded). The pooled spectral estimates (Fig. 6) indicate the relative power (variance) of the tremor at each Fourier frequency and provide a concise description of the characteristics of the tremor for all records in each condition. These pooled spectral estimates exhibit the same load dependency as those obtained from individual subjects (Stiles and Randall 1967). In both conditions the dominant spectral component, which can be taken as an indication of the dominant tremor rhythm, is the load-dependent mechanical resonance component. This has an average frequency of 23 Hz for the unloaded data set and 17 Hz for the loaded data set. These frequencies overlap with the 15- to 30-Hz band of motor-unit synchronization, therefore the load-independent contribution to physiological tremor from rhythmic motor-unit activity in this frequency range cannot be identified from examination of tremor spectra. The pooled coherence estimates (Figs. 4, *B* and *C,* and 5, *B* and *C*), however, provide an estimate of the contribution to the tremor from motor-unit activity, at each frequency. These indicate that a single motor-unit discharge can account for between 4 and 10% of the tremor signal in the two frequency bands 1–12 Hz and 15–30 Hz. In some subjects coherence estimates between single motor units and tremor for single records had values up to 0.4, indicating that, in some cases, an individual motor unit (and all those correlated with it) can predict up to 40% of the tremor signal at these frequencies. Examples of coherence estimates between single motor units and tremor for single records drawn from the present data sets are shown in Conway et al. (1995a), Halliday et al. (1995b), and Amjad et al. (1997). A natural question to ask of this analysis is "are the effects uniform across subjects?" In other words, is pooled coherence an appropriate tool to apply to the present data? As part of the analysis, we estimated the pooled motor unit to motor-unit coherence for each subject (by combining all records from each subject) and plotting histograms of the peak coherence in the 1- to 12-Hz and 15- to 30-Hz frequency bands for each subject. These histograms were well fit by a normal distribution (assessed by constructing normal probability plots and summary statistics for each set of values) indicating a range of values distributed around a central value. Therefore for the present data, intersubject variability leads to a range of strengths of motor-unit synchronization, which appears normally distributed. Under these conditions, pooled coherence is an appropriate tool to estimate the average strength of correlation at each frequency across subjects. In addition, the presence of the same two load-independent frequency bands can be inferred from coherence estimates between pairs of motor units, and between single motor units and tremor from single subjects (Conway et al. 1995a), as in the present analysis across subjects.

The pooled coherence estimates between the rectified surface EMG and tremor (Figs. 4D and 5D) have a larger magnitude and indicate that on average, the rectified surface EMG can account for 20% of the tremor signal in the two frequency bands 1–12 Hz and 15–30 Hz. This increase in magnitude over

the pooled coherence for a single motor-unit discharge may be due to the surface EMG containing information representing the discharge of many motor units. Thus the surface EMG that samples a pool of the active motor units in EDC is able to account for more of the tremor signal in the two frequency bands at which the motor-unit discharges are correlated. In some subjects coherence estimates between rectified EMG and tremor for single records had values up to 0.7, indicating that the surface EMG can account for 70% of the tremor signal in these frequency bands. These examples were generally obtained from subjects who had stronger motor-unit synchronization. An example of coherence between rectified surface EMG and tremor is given in Halliday et al. (1995b).

Using a similar approach based on coherence estimates, Padsha and Stein (1973) estimated that surface EMG activity in finger extensor muscles could account for ~11% of the tremor activity at frequencies up to 10 Hz. Our pooled coherence estimates between surface EMG and tremor consider the relationship between motor-unit activity and tremor over a wider range of frequencies, and suggest that, on average, ~20% of the tremor signal in the frequency bands 1–12 Hz and 15–30 Hz can be accounted for by EMG activity in a single muscle.

Relationship between physiological tremor and motor-unit synchronization

We have demonstrated that correlation between motor-unit activity and tremor occurs in the same two frequency bands as the correlation between motor units (Figs. 4 and 5). Partial coherence analysis demonstrates that motor-unit synchronization is the source of the rhythmic contributions to normal physiological tremor in these two frequency bands (Fig. 7). Previous studies on motor-unit synchronization and tremor used a time domain approach based on comparison of the magnitude of the central peak in the cross-correlation histogram with either peak-to-peak tremor magnitude (Dietz et al. 1976) or RMS tremor magnitude (Logigian et al. 1988; Semmler and Nordstrom 1995, 1998). It is therefore difficult to reconcile these previous studies of the relationship between motor-unit synchronization and tremor with the present analysis, which is based on a frequency domain approach. A frequency domain analysis may be more suited to charcterize the relationship between the different rhythmic components of physiological tremor and motor-unit synchronization. The present study demonstrates, using a statistically rigorous protocol (Amjad et al. 1997; Halliday et al. 1995b), that two distinct rhythmic components of normal physiological tremor are related to motor-unit synchronization. We therefore conclude that motor-unit synchronization contributes to normal physiological tremor, and not just to cases of enhanced tremor as claimed in Freund (1983).

Elble and Randall (1976) did study the relationship between motor-unit firing and tremor in the frequency domain. They considered tremor in force records recorded from the extended middle finger and used forces of 200–250 g, to maximize the 8- to 12-Hz component of tremor, which resulted in patterns of motor-unit firing containing transient sequences of double discharges consisting of alternating short and long intervals (see Fig. 2, Elble and Randall 1976). Under these conditions, they obtained coherence estimates between both surface EMG and tremor and single motor units and tremor, which were re-stricted to the frequency range 8–12 Hz. The double discharge patterns of motor-unit firing observed by Elble and Randall (1976) may be a consequence of the larger force exerted by their subjects compared with the present study. Such motor-unit activity was not observed in our data (Fig. 1). Fox and Randall (1970) observed a 10-Hz peak in the spectra of forearm tremor and rectified, filtered biceps EMG, which was only present with the addition of 10-lb load to the wrist, and was not present with smaller loads. In recordings of forearm tremor and biceps and brachioradialis EMGs, made under conditions of compliant loading, Matthews and Muir (1980) observed a large coherence at 10 Hz between the tremor and rectified, filtered EMG only during recordings made with large force levels. In a study of the frequency components present in tremor recordings, surface EMG and muscle vibration in subjects making contractions of up to 50% MVC against an elastic load, McAuley et al. (1997) observed peaks in coherence estimates around 10, 20, and 40 Hz between the signals. It is therefore possible that the pattern of motor-unit synchronization may alter when large force levels are used. Although our pooled coherence estimates extend to frequencies above 40 Hz, there is no evidence of a distinct frequency band around 40 Hz in the motor-unit synchronization, or in the correlation between motor-unit activity and tremor (see Figs. 4 and 5) (McAuley et al. 1997, Fig. 4). Given these differences in motor-unit and EMG firing patterns, it is difficult to generalize from the above results to the present study, and vice versa. Indeed Elble and Randall (1976) point out that their observed pattern of motor-unit firing cannot be assumed to be present in other muscles. Nevertheless, there are similarities between the results of Elble and Randall and the present study: both observed a relationship between motor-unit activity and finger tremor in a preferred frequency range, which is not related to motor-unit firing rate.

Physiological tremor and surface EMG as predictors of motor-unit synchronization

We have demonstrated that components in normal physiological tremor are due to motor-unit synchronization in two frequency bands. The corollary to this result is that normal physiological tremor can be used as a predictor of motor-unit synchronization in the two frequency bands 1–12 Hz and 15–30 Hz. On this basis a statistical spectral analysis undertaken using a tremor acceleration signal can be used as a predictor of motor-unit synchronization in these frequency bands within the muscles that contribute to the tremor (Halliday et al. 1995b).

Rectified surface EMG, when processed according to the methods in Halliday et al. (1995b), is a powerful predictor of the presence of distinct frequency bands in motor-unit synchronization (Fig. 7, *B* and *D*). Previous studies on estimating motor-unit synchronization from a surface EMG signal have used time domain averaging techniques (Milner-Brown et al. 1973), which compare spike-triggered averages of unrectified and rectified EMG. This approach is based on a specific model describing the relative contributions of synchronized and background motor-unit activity to raw and rectified EMG averages (Milner-Brown et al. 1973). This method has limitations in its use; the model has two major sources of error related to the nonlinear relation between rectified and unrectified EMG, and the index is sensitive to the background level of surface EMG

(Yue et al. 1995). In contrast, the complete reduction over the 15- to 30-Hz frequency range in the estimated partial coherence between the motor units with rectified surface EMG as predictor (Fig. 7, *B* and *D*) demonstrates that rectified surface EMG can be used as a statistical predictor of motor-unit synchronization in a multivariate Fourier analysis (Halliday et al. 1995b), under experimental conditions similar to those in the present study.

Figure 7 illustrates that tremor and surface EMG signals are equally good predictors of motor-unit synchronization. Physiological tremor and surface EMG recordings are therefore rich signals that contain information related to rhythmic components associated with motor-unit synchronization, within single muscles (EMG) and agonist muscle groups (tremor).

Relationship between unrestrained limb tremor and isometric force tremor

The present study considers tremor during postural contractions involving position holding of the unrestrained finger against gravity. Many previous studies have considered tremor in force recordings during isometric contractions. Halliday and Redfearn (1956) pointed out that the characteristics of tremor will depend on how it is measured. The dominant mechanical resonance component in acceleration recordings of postural tremor (Stiles and Randall 1967) is damped out in isometric contractions against a force transducer (Allum et al. 1978; Elble and Randall 1976; Hömberg et al. 1986). The mechanical resonance component reflects activation of a resonant system by motor-unit activity (Stiles and Randall 1967), or other external perturbations to the limb segment.

The presence of an 8- to 12-Hz load-independent component of physiological tremor has been reported in postural tremor of the unrestrained finger (Halliday and Redfearn 1956; Stiles and Randall 1967) and in force recordings during isometric contractions (Allum et al. 1978; Elble and Randall 1976). Brown et al. (1982) observed an 8- to 11-Hz rhythmicity in force recordings obtained under isometric conditions and conditions of low inertial compliant loading during thumb flexion. The 1- to 12-Hz and 15- to 30-Hz components of motor-unit synchronization that we have described for the present data are also present in motor-unit pairs recorded under isometric force conditions (Farmer et al. 1993). Although different types of contraction (postural or isometric) have a strong effect on the characteristics of the resultant tremor signal, the 1- to 12-Hz and 15- to 30-Hz rhythmic components of motor-unit synchronization are present in both types of contraction at low force levels.

Allum et al. (1978) and Hömberg et al. (1986) have suggested that the load-independent component observed in isometric force tremor spectra relates to the firing rate of unfused motor units. This suggestion is based only on examination of tremor spectra. The present study considers the correlation between a large population of single motor-unit discharges and shows no dependence on firing rate (Figs. 4, *B* and *C,* and 5, *B* and *C*). Examination of tremor spectra alone will fail to reveal contributions from the 15- to 30-Hz rhythmic component of motor-unit synchronization. Hömberg et al. (1986) suggest that tremor is a useful predictor of motor-unit activity and reflects firing rates of active motor units in isometric force tremor. The present data alternatively suggest that unrestrained postural tremor reflects rhythmic processes related to motor-unit synchronization within active pools of motor units, and not asynchronous activity relating to motor-unit firing rates.

Neural structures relating to normal postural physiological tremor

The presence of an 8- to 12-Hz load-independent component in physiological tremor that is correlated with motor-unit activity has been well documented (Elble and Randall 1976; Halliday and Redfern 1956; Stiles and Randall 1967). In the present study, we have observed a load-independent component of motor-unit synchronization that includes this frequency range and extends down to lower frequencies. However, the lowest frequency components in this 1- to 12-Hz range are not as strong in the pooled motor unit to tremor or pooled surface EMG to tremor coherence estimates for both the unloaded (Fig. 4, *B–D*) or loaded (Fig. 5, *B–D*) data sets, when compared with other frequencies in this range. These lowest frequency components in the motor-unit synchronization could result from common slow rate modulation of motor-unit firing rates during the postural task. This slow trend in the mean rate will appear as an increase in the lowest frequencies in coherence estimate between the two motor units (e.g., see Fig. 2, *A* and *C*). Such trends in point process interval values cannot be easily removed (unlike trends in amplitude values in time series data). Therefore the 1- to 12-Hz component of motor-unit synchronization may contain contributions from two different sources, one of which reflects common rate modulation of motor-unit pairs during the maintained postural tasks and occurs at the lowest frequency components (DeLuca et al. 1982; Farmer et al. 1993). The higher frequency components in this 1- to 12-Hz range overlaps with the previously reported 8- to 12-Hz load-independent component of physiological tremor. It is in this frequency range that the pooled partial coherence estimates exhibit the largest reduction in magnitude using the tremor as predictor, indicating a clear contribution from motor-unit synchronization to the tremor.

Recent work on the origin of this 8- to 12-Hz rhythmic load-independent component of physiological tremor has suggested the presence of an 8- to 12-Hz oscillator. A number of theories have been proposed for the location of such an oscillator. Elble and Randall (1976) proposed Renshaw inhibition. Llinás and co-workers have suggested inhibition-rebound excitation oscillations in the inferior olive as the source of these oscillations (Llinás 1984). Other authors have suggested the thalamus or cerebellum as structures involved in generating the 8- to 12-Hz component (for a review see Elble and Koller 1990). The present results demonstrate a load-independent contribution to postural finger tremor from motor-unit synchronization in this frequency range and provide strong evidence in support of an 8- to 12-Hz central generator. However, the present experiments cannot provide any evidence in favor or against any of the above origins of such an 8- to 12-Hz oscillator.

The involvement of the stretch reflex in physiological tremor remains unclear. Early studies suggested that oscillations in the stretch reflex were the source of the 8- to 12-Hz load-independent component of finger tremor (Halliday and Redfearn 1956; Lippold 1970). The evidence against this has been well documented (see, e.g., Elble and Koller 1990; Elble and Randall

1976; Freund 1983). In particular, the frequency of the oscillations is independent of the conduction time around the reflex loop; 8- to 12-Hz load-independent oscillations have been observed in tremor and EMG recordings from finger (Elble and Randall 1976; Halliday and Redfearn 1956), elbow (Fox and Randall 1970), and foot (Mori 1973) muscles. Several authors have, however, suggested that oscillations in the reflex loop are a mechanism underlying enhanced or activated larger amplitude physiological and pathological tremor (Freund 1983; Logigian et al. 1988). Hagbarth and Young (1979) demonstrated that human muscle spindle primary endings have sufficient sensitivity to respond to normal physiological tremor. The present results demonstrate that 1- to 12-Hz and 15- to 30-Hz load-independent components in motor-unit synchronization can be detected in normal postural finger tremor, with the likely result of afferent discharges being modulated by these components. In a study of the relationship between torque and Ia afferent in humans during weak isometric contractions, Halliday et al. (1995a) observed a preferential transmission of frequencies, which was not related to motor-unit firing rates, with the torque signal modulating the afferent discharge in the frequency range 5–11 Hz. However, Wessberg and Vallbo (1996) examined the timing and strength of reflex effects during voluntary finger movements and concluded that the stretch reflex cannot account for the 8- to 10-Hz modulation of EMG activity observed during finger movements (Vallbo and Wessberg 1993).

The present study provides the first direct demonstration of the involvement of a 15- to 30-Hz component of motor-unit synchronization in normal physiological tremor, which can be predicted through the use of a surface EMG signal (Fig. 7, *B* and *D*). Conway et al. (1995b) demonstrated that cortical activity recorded from the hand area of the sensorimotor cortex was correlated with surface EMG from 1DI during a maintained contraction. These correlations occurred mostly in the frequency range 15–30 Hz, and they concluded that this represented a contribution to motor-unit synchronization related to the performance of postural tasks and suggested that these frequencies also contribute to physiological tremor. Similar correlations have been reported between cortical activity and biceps EMG and cortical activity and foot flexor EMG (Salenius et al. 1997) and between cortical activity and wrist extensor and flexor muscles during postural tasks (Halliday et al. 1998). Therefore the 15- to 30-Hz rhythmic component of motor-unit synchronization that contributes to physiological tremor is related to rhythmic cortical activity.

Definition of normal physiological tremor

We conclude by proposing a revised definition of physiological tremor, recorded as an acceleration signal, during low force contractions involving extension of the unrestrained finger against gravity. The traditional view of such a signal is that it contains two rhythmic components: a mechanical resonance component (around 15–30 Hz) and a load-independent rhythmic component around 8–12 Hz (Elble and Randall 1976; Halliday and Redfearn 1956; Stiles and Randall 1967). These two rhythmic components can be identified by examination of the estimated tremor spectrum. In the present study we have used spectral correlation methods to identify rhythmic components in motor-unit activity that also contribute to physiological tremor, which cannot be identified by inspection of the tremor spectrum. Using this approach, the present data have identified the presence of a third component in tremor during postural contraction of finger muscles against gravity: a 15- to 30-Hz load-independent component, which is masked by the mechanical resonance component of the tremor, but which can be identified from correlation between motor-unit activity and tremor. Both the load-independent components at 8–12 Hz and 15–30 Hz reflect rhythmic components of motor-unit synchronization and are not related to motor-unit firing rates. Importantly, the latter is expressed at the level of the motor cortex (Conway et al. 1995b; Halliday et al. 1998; Salenius et al. 1997) and may reflect a component of the motor command associated with the performance of postural tasks.

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