

Motor-Unit Activity Responsible for 8- to 12-Hz Component of Human Physiological Finger Tremor

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TO ESTABLISH A TREMOR as neurological in origin, one must demonstrate a synchronous motor-unit activity that is correlated with the tremor. Whether the 8- to 12-Hz component of human physiological finger tremor is correlated with a synchronous 8- to 12-Hz motor-unit activity has been a subject of debate since the observations of Lippold et al. (25). These investigators observed 8- to 12-Hz bursts of motor-unit activity in skin and wire electromyograms of a variety of skeletal muscles during steady voluntary contractions, and it is during such contractions that an 8- to 12-Hz tremor has been recorded from the extended third digit (16, 23), the partially flexed forearm (12), the abducted index finger (37), and the soleus during quiet standing (25, 33). However, Taylor (40) has since demonstrated that such bursts of motor-unit activity could be a chance phenomenon, representing no true tendency toward synchronization. Furthermore, Taylor's work established the necessity of rigorous statistical methods in analyzing electromyograms (EMGs) for synchronization, the visual analysis used by Lippold et al. (25) being inadequate.

Lippold et al. (25) were unable to define the activities of individual motor units. Since their study, several investigators have performed statistical studies of human motor-unit spike trains recorded during steady voluntary contractions (21, 30, 33, 36). Of these investigators, only Mori (33) found a tendency toward synchronization of contiguous motor units. The muscle studied was the soleus during quiet standing, and Mori found the motor units to fire synchronously at approximately 9 spikes/s.

Although the individual motor-unit activity responsible for the 8- to 12-Hz component of human physiological finger tremor is virtually unknown, recent evidence suggests a correlation between this tremor and the extensor digitorum surface EMG (34). In this paper, we rigorously establish the existence of an 8- to

12-Hz amplitude modulation in the extensor digitorum communis surface EMG, and we demonstrate the statistical correlation of this modulation with the 8- to 12-Hz component of finger tremor, as suggested by Lippold et al. (23, 25). In addition, we define the firing patterns of individual extensor digitorum motor units responsible for this 8- to 12-Hz modulation and tremor. Contrary to past speculation (2, 22), the 8- to 12-Hz component of finger tremor is not simply the result of synchronous motor units firing at 8-12 spikes/s for, in addition to motor units firing in this frequency range, motor units firing at 13-22 spikes/s also contribute as a result of grouped discharges within single motor-unit spike trains. Indeed, in our experiments, motor units firing at 8-12 spikes/s were the exception rather than the rule.

METHODS

All tremor measurements were made with a Grass model FT.03 force transducer. This recording system had a resonant frequency of 330 Hz, well beyond the 0- to 30-Hz range of finger tremor. The subject sat in a sturdy wooden chair with his arm abducted at 45° from the midline. The pronated forearm was extended horizontally at right angles to the arm and was supported by a sturdy lab bench and foam-rubber pad. All tremor measurements were taken from the distal phalanx of the third digit during voluntary, horizontal extension against the force transducer. The remainder of the pronated hand was secured to the lab bench. The signal from the force transducer was passed through a band-pass filter of 2.5-30 Hz to remove the prominent tension oscillations in the 0- to 2.5-Hz range, and the resulting signal was recorded on an FM channel of a Hewlett-Packard 3960 tape recorder (passband 0 Hz to 5 kHz).

All EMG recordings were taken from that portion of the extensor digitorum communis most responsible for extension of the third digit. This area of the muscle was initially located

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through palpation during voluntary contraction and was verified electromyographically after placement of the electrodes. For surface electromyography, two 1.0-cm diameter Beckman skin electrodes were positioned about 1.5-2.0 cm apart in the direction of the muscle fibers, resulting in a bipolar recording. The ground electrode was positioned on the flexor surface of the forearm. The skin-electrode leads were fed to a differential amplifier with a gain of 100 and a passband of 10 Hz to 3 kHz. The output of the differential amplifier was further amplified and recorded on an FM channel of the Hewlett-Packard tape recorder (passband 0 Hz to 5 kHz).

Motor-unit spike trains were recorded using a specially constructed bipolar needle electrode. This electrode was inserted between the two recording skin electrodes and fastened securely in place. The ground for this needle electrode was a skin electrode positioned on the upper arm or on the anterior tibial surface of the leg. The needle electrode leads were passed to a differential amplifier with a gain of 100 and a passband of 100 Hz to 10 kHz. The output of this differential amplifier was further amplified, filtered with a 60-Hz band-reject filter, and recorded on the direct channel of our tape recorder (passband 70 Hz to 60 kHz).

During each experiment the surface EMG, tremor, and needle EMG were continuously monitored on a storage oscilloscope. The needle electrode was patiently positioned such that at least one motor-unit spike train could be faithfully followed among the background interference of other more distant motor units. The high selectivity of the bipolar needle electrode kept the level of this interference at a very tolerable minimum. All data were recorded on the tape recorder at 15 inches/s and later played back at 0.1 speed for analysis purposes.

Individual motor-unit spike trains were distinguished and followed via the standard criteria of size and shape of the motor-unit action potential. The tape-recorded spike trains were digitized at 10,000 samples per second on a PDP-12 computer, and successive interspike intervals (ISIs) of a given motor unit were computed using a program designed to recognize a specified motor-unit action potential on the basis of these criteria. All such computer computations were manually double-checked, and ISI sequences with questionable ISIs were not used for further analysis. Less than 25% of the spike trains recorded had to be discarded. Although serial ISIs were computed for the recorded motor units over periods as long as 70 s, such long ISI sequences were analyzed in 13-s epochs, containing from 130 to 280 action po-

tentials. By dividing a long spike train into 13-s epochs, the effects of slow trends in mean firing frequency were minimized while still retaining sizable ISI sequences for analysis.

Prior to frequency analysis, the surface EMG was full-wave rectified and low-pass filtered (-3 dB at 21 Hz), resulting in a signal dubbed the "demodulated EMG" by Fox and Randall (12). The demodulated EMG has been shown to be proportional to the isometric tension exerted by a muscle (19) and is approximately the envelope of the surface EMG. Therefore, frequency analysis of the demodulated EMG provides a measure of any rhythmical variations in the amplitude of the surface EMG within the frequency band of the low-pass filter. All finger tremor and demodulated EMG signals were digitized on the PDP-12 computer at 100 samples per second and subjected to the well-known methods of spectral analysis (5).

The studies described in this paper constitute a total of 24 experiments involving a total of six healthy volunteers (five male and one female, ages 20-50 yr). However, for reasons given in the RESULTS, 17 of these experiments and all of the data presented in this paper came from four of the six subjects (three male and one female, ages 20-30 yr). Forty-three motor-unit spike trains were analyzed in this study.

Because the demodulated EMG and tremor were more meaningfully analyzed in the frequency domain and because the primary purpose of this study was to relate the activities of individual motor units to the demodulated EMG and tremor, motor-unit spike trains were treated as stochastic point processes, and autospectral analysis of individual spike trains was performed using the methods first described by Bartlett (4). For a spike train of duration T , containing M action potentials, the Fourier-Stieltjes transform of the spike train is given in *equation 1*, where t_j ($j = 1, 2, 3, \dots, M$) is the time of occurrence of the j th action potential and ω_p is the p th harmonic ($\omega_p = 2\pi p/T$ and $p = 1, 2, 3, \dots$) (10).

$$H(\omega_p) = \frac{1}{\sqrt{\pi T}} \left[\sum_{j=1}^M \cos(t_j \omega_p) + i \sum_{j=1}^M \sin(t_j \omega_p) \right], \quad i = \sqrt{-1} \quad (1)$$

Having calculated $H(\omega_p)$, the estimated spectral density (autospectrum), $I(\omega_p)$, of the spike train was computed using *equation 2*, where $H^*(\omega_p)$ is the complex conjugate of $H(\omega_p)$ (10).

$$I(\omega_p) = H(\omega_p)H^*(\omega_p) \quad (2)$$

The estimated spectral density was smoothed over K harmonics to obtain statistically consis-

tent estimates. Although a variety of smoothing procedures is available (10), the procedure followed was to average continuous harmonics in groups of K , resulting in L nonoverlapping smoothed spectral estimates, $\bar{I}(\omega_L)$. When multiplied by $2\pi T/M$, these smoothed estimates are approximately independent chi-squared random variables with $2K$ degrees of freedom. The value of K is somewhat arbitrary but is restricted by the desired frequency resolution and the necessary statistical reliability. The value of L , in turn, depends on the number of harmonics calculated, and although the total number of harmonics is mathematically unlimited, statistical limitation should be imposed when testing statistical hypotheses (4, 10).

To test for possible correlation between the frequency components of two spike trains, $X(t)$ and $Y(t)$, or between a spike train, $X(t)$, and a continuous stochastic process, $Y(t)$ (e.g., tremor or the demodulated EMG), the estimated cross-spectrum, $I_{XY}(\omega_p)$, and coherency spectrum, $K_{XY}(\omega_L)$, were computed using equations 3 and 4, respectively (9, 20).

$$I_{XY}(\omega_p) = H_X(\omega_p)H_Y^*(\omega_p) = C_{XY}(\omega_p) - iQ_{XY}(\omega_p) \quad (3)$$

$$K_{XY}(\omega_L) = \bar{I}_{XY}(\omega_L)\bar{I}_{XY}^*(\omega_L) / [\bar{I}_X(\omega_L)\bar{I}_Y(\omega_L)] \quad (4)$$

In calculating the coherency spectrum, the amplitude squared of the smoothed cross-spectrum is normalized by dividing by the product of the smoothed autospectra and, in doing so, the correlation squared between X and Y at a given frequency is placed on a scale of zero to one. The cross-spectral estimates were smoothed by averaging contiguous harmonics in groups of K , resulting in L nonoverlapping smoothed estimates, $\bar{I}_{XY}(\omega_L)$. Throughout this paper, the coherency spectrum was assigned the value of zero at all frequencies at which either autospectrum had a value that was statistically zero. In calculating the confidence limits for the coherency spectrum, we have followed the procedure discussed by Bendat and Piersol (5) for continuous stochastic processes.

Given the smoothed estimated cross-spectrum, the phase-spectrum between two stochastic processes was determined using equation 5, where $\bar{Q}_{XY}(\omega_L)$ and $\bar{C}_{XY}(\omega_L)$ are the smoothed imaginary and real parts of $\bar{I}_{XY}(\omega_L)$, respectively (20).

$$\phi(\omega_L) = \tan^{-1}[\bar{Q}_{XY}(\omega_L) / \bar{C}_{XY}(\omega_L)] \quad (5)$$

For convenience we have omitted the vertical axes from all autospectra presented in this paper. These autospectra show how the total variance of a sampled signal (e.g., tremor or a

spike train) is distributed over frequency, and the absolute magnitude of this variance would be of little value in the following discussion.

RESULTS

Finger tremor and surface EMG

In Fig. 1 sample tremor and surface EMG records are displayed, as recorded from the horizontally extended third digit and the extensor digitorum, respectively. During this experiment the subject was able to monitor mean voluntary tension via an oscilloscope tracing and was instructed to exert a steady tension of approximately 200–250 g. Voluntary exertion of this magnitude tended to maximize the amplitude of the 8- to 12-Hz tremor, and throughout the experiments described in this paper, advantage was taken of this property in order to obtain tremor and EMG records of optimal magnitudes. Such accentuation of this tremor by increased strength of contraction has been widely demonstrated (17, 37, 39).

In addition to the tremor oscillations at 8–12 Hz, prominent large-amplitude oscillations occurred in the range of 0–5 Hz, and to enable greater amplification before computer digitization, all tremor signals were high-pass filtered, thereby removing the oscillations in the range of 0–2.5 Hz. In following this procedure we did not wish to imply that these low-frequency oscillations were of no physiological importance; we were merely focusing our attention on the 8- to 12-Hz tremor. It should be noted that this filtering procedure produced an artificial spectral peak at about 2.5 Hz (Fig. 1).

The 8- to 12-Hz tremor oscillations resulted in a prominent peak in tremor spectrum (Fig. 1). In addition, the simultaneously recorded EMG exhibited periods of pronounced rhythmic bursting at 8–12/s. Visual examination of longer EMG records revealed that the intensity of this bursting activity waxed and waned with time and, in order to eliminate the subjectivity of visual analysis, we have computed the spectrum of the demodulated EMG (Fig. 1). This spectrum contains a large amount of activity at 8–12 Hz, relative to the activity at the neighboring frequencies of 0–25 Hz, and it confirms the presence of an 8- to 12-Hz modulation in the amplitude of the surface EMG. A statistical correlation between this modulation and the 8- to 12-Hz tremor was readily proved by coherency analysis. The coherency spectrum of Fig. 1 exhibits a coherency of 0.92 (192 df) at 10.6 Hz, firmly establishing such a correlation. Phase analysis revealed that the 8- to 12-Hz tremor (peaks in finger extension) lagged the

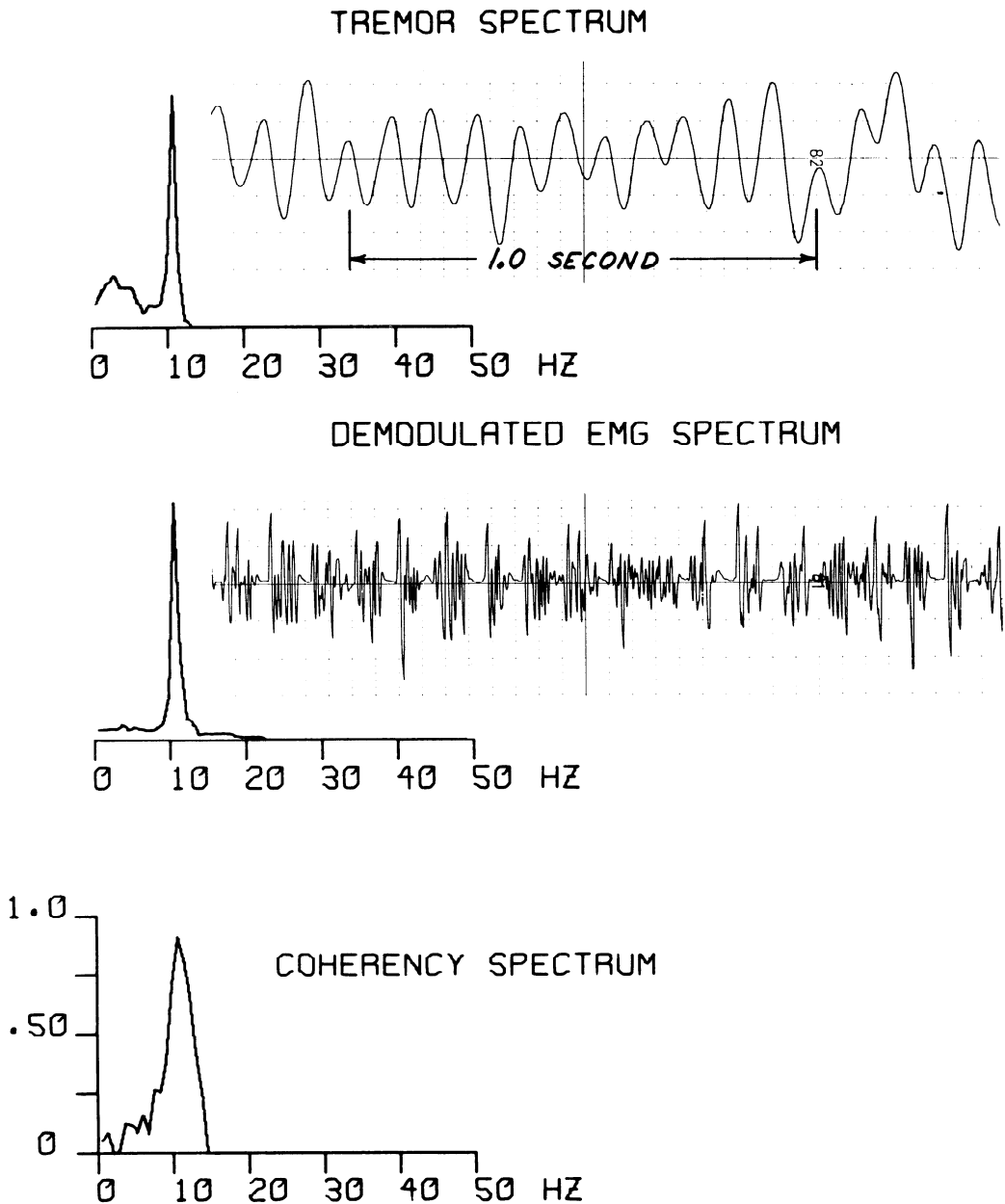


FIG. 1. Coherency analysis of simultaneously recorded finger tremor and demodulated EMG records (123 s of data). Samples of tremor and the surface EMG are displayed with the tremor spectrum and demodulated EMG spectrum, respectively. Increased tension is an upward deflection in the tremor record. Each coherency value has 192 df, and coherencies greater than 0.032 are significant at the 99% confidence level. Subject *RJE*.

EMG modulation (bursts of EMG activity) by $180 \pm 5^\circ$, a measurement consistent with an earlier study (34).

Earlier population studies revealed that the amplitude of this tremor varies greatly from person to person (17). Of the six subjects used

in our experiments, four presented with a tremor and EMG modulation similar to those of Fig. 1. Although the 8- to 12-Hz tremor could be demonstrated in the remaining two subjects, the amplitude of this tremor was very small, and the 8- to 12-Hz surface EMG modulation in

these subjects was barely detectable, despite the sensitivity of our recording and analysis techniques. Consequently, these two subjects were not used extensively in the following experiments.

Individual motor-unit activity responsible for 8- to 12-Hz tremor

Having established a modulation in the surface EMG amplitude that is correlated with the 8- to 12-Hz finger tremor, we now turn to the problem of what type of individual motor-unit activity is responsible for this modulation and tremor. Our experimental approach to this problem consisted of simultaneously recording bipolar skin and needle EMGs of the extensor digitorum while horizontally extending the third digit. In some experiments tremor was also measured, the mean voluntary tension being approximately 200–250 g. When tremor was not measured, 200 g were suspended from the terminal phalanx of the third digit in order to maximize tremor and the responsible motor-unit activity.

To introduce the type of motor-unit activity responsible for the 8- to 12-Hz tremor, we have selected the large motor unit in Fig. 2. The firing pattern exemplified by this motor unit produced the greatest 8- to 12-Hz activity of all patterns recorded in our experiments (as determined by spectral analysis), and this pattern deviated markedly from the more-or-less rhythmical pattern of firing that has been considered characteristic of tonic motor units during steady isometric contractions (8, 13, 21, 36). In particular, transient episodes of grouped discharges of a single motor unit could be observed (Fig. 2). During these episodes interspike intervals of 8–30 ms alternated with interspike intervals of 60–90 ms, and in no instance was a grouped discharge observed to consist of more than two motor-unit action potentials. Spectral analysis of this spike train revealed that this grouped ("double") discharge-firing pattern produced a spectral peak at 8–12 Hz, in addition to the expected spectral peak at the mean firing frequency of 21 spikes/s (Fig. 2). Although the intensity of this action-potential grouping waxed and waned with time, a correlation between these grouped discharges and the surface EMG modulation was sometimes evident through mere visual inspection. However, in order to rigorously demonstrate an association between the 8- to 12-Hz activities of the single motor-unit spike train and demodulated EMG, we calculated the coherency spectrum of Fig. 2 which shows strong coherency at 8–12 Hz and negligible coherency at all other frequencies.

Forty-three motor-unit spike trains were recorded and analyzed in this manner, and these spike trains had mean firing frequencies ranging from approximately 10–22 spikes/s. Of the 24 spike trains having mean firing frequencies of 17–22 spikes/s, 12 produced 8- to 12-Hz spectral peaks in addition to the expected spectral peaks at the mean firing frequencies. These 12 motor units were recorded from four of our six subjects and exhibited the above double-discharge pattern of firing. The remaining motor units in this frequency range displayed the well-known rhythmical firing pattern. Not surprisingly, the magnitudes of adjacent interspike intervals were correlated in the range of 0.5 to 0.9 for all spike trains exhibiting the double-discharge firing pattern (significant at the 95% confidence level). The 12 rhythmically firing motor units in the 17–22 spikes/s range produced first-order correlation coefficients in the range of –0.2 to –0.6 (significant at the 95% confidence level). In light of these large correlation coefficients, one can no longer categorize all normal tonic motoneuron interspike-interval sequences as renewal processes (13) since many clearly are not (21).

Of the 43 motor units, 19 had mean firing frequencies of approximately 10–17 spikes/s, and 10 of these motor units produced statistically significant spectral peaks at 8–12 Hz. All motor units in this range of mean firing frequencies were found to exhibit little or no correlation between adjacent interspike intervals. Indeed, the correlation between adjacent interspike intervals was always less than –0.35 and was often statistically zero. Although included in this group, motor units firing at 10–12 spikes/s were encountered only twice in our experiments, and one of these two motor units was not correlated with the 8- to 12-Hz tremor.

Of the 17–22 spikes/s motor units with 8- to 12-Hz spectral peaks, a double discharge was usually produced during a surface EMG burst. However, the 10–17 spikes/s motor units often fired only once per burst, and when these slower motor units did fire twice per burst, the interspike intervals of the grouped discharges were characteristically not as short (approximately 20–40 ms) as those of the 17–22 spikes/s motor units. Thus, while both groups of motor units exhibited an 8- to 12-Hz modulation in the probability of firing, the modulation of the 10–17 spikes/s group was much less obvious on visual inspection. The motor unit in Fig. 3 is an example of this type of motor-unit activity and, like the more rapidly firing motor unit of Fig. 2, this motor unit produced a spectral peak at 8–12 Hz and at its mean firing frequency of 13.8 spikes/s. Coherency analysis revealed a strong

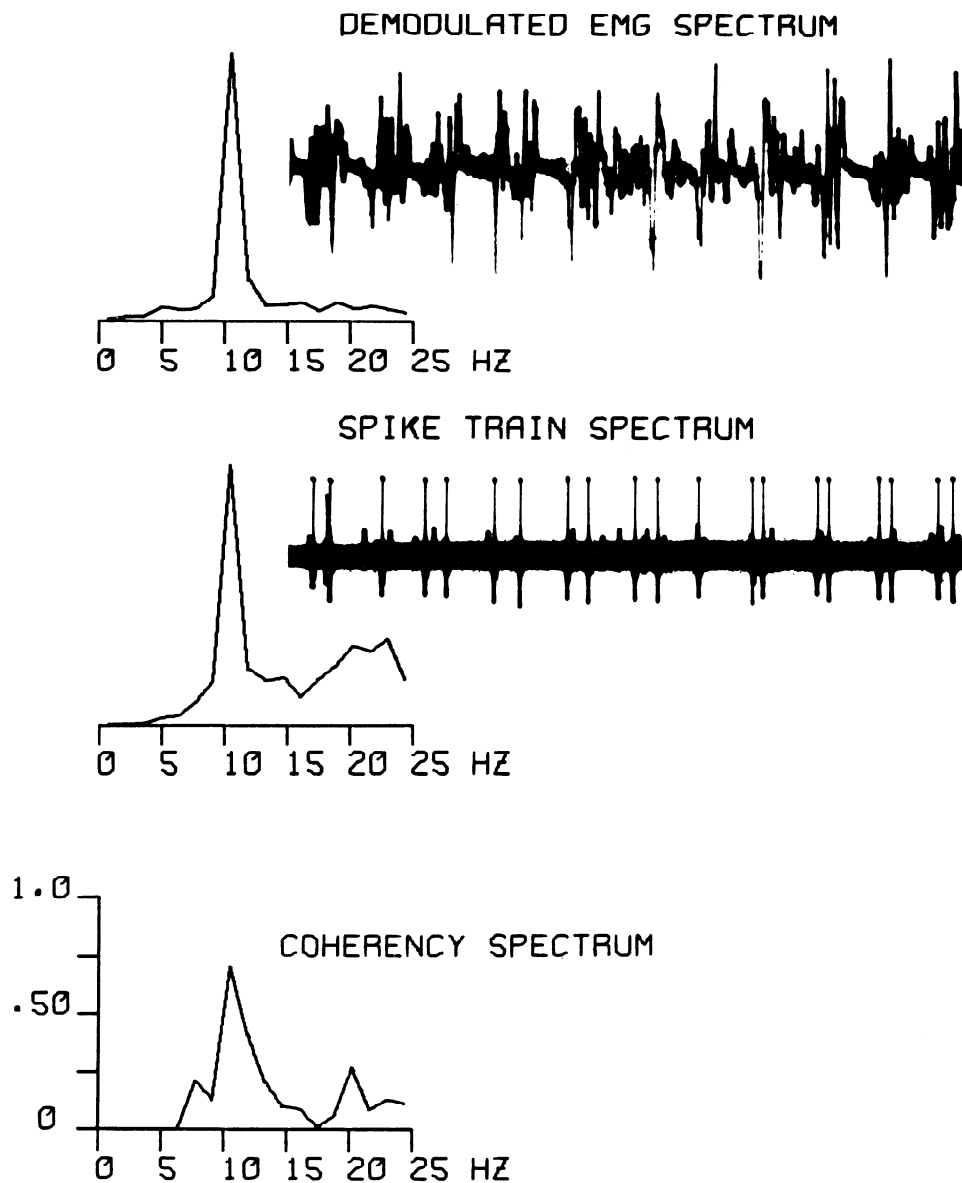


FIG. 2. Coherency analysis of simultaneously recorded motor-unit spike train and demodulated EMG records (13 s of data). Sample records (1.0 s in duration) of the spike train (the large spikes) and the surface EMG are displayed with the spike-train spectrum and demodulated EMG spectrum, respectively. Each coherency value has 36 df, and coherencies greater than 0.15 are statistically significant at the 99% confidence level. Subject *RJE*.

correlation between this 8- to 12-Hz activity and the 8- to 12-Hz amplitude modulation in the surface EMG.

Thus, two somewhat arbitrarily defined groups of motor-unit firing patterns have been described, both of which contribute to the surface EMG bursting (amplitude modulation) that has been shown to be strongly correlated with the 8- to 12-Hz finger tremor. However, it

should be emphasized that only 22 of the 43 motor units recorded were found to participate in this 8- to 12-Hz rhythm. In Fig. 4, the auto-spectra of 12 motor units are shown, all recorded during several identical experiments involving four subjects. In the first two columns are shown the spectra of six motor units of various mean firing frequencies, and all have 8- to 12-Hz spectral peaks in addition to peaks at the

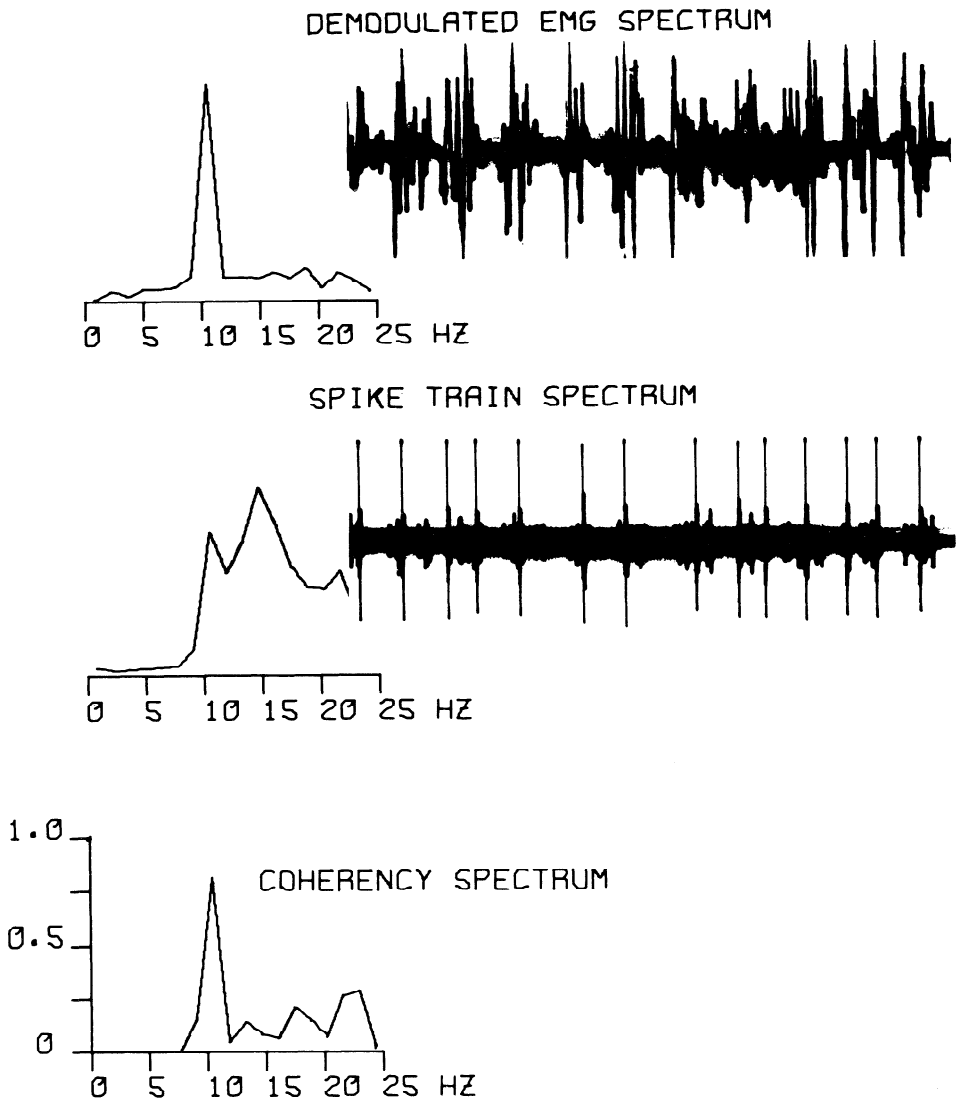


FIG. 3. Same as Fig. 2. Note that this motor unit exhibits an 8- to 12-Hz modulation that is much less obvious than that of the motor unit in Fig. 2.

mean firing frequencies. The second two columns are composed of autospectra of motor units that fired more or less rhythmically and, consequently, these spectra have peaks at the mean firing frequencies only.

Of course, motor units displaying the 8- to 12-Hz rhythm were more readily recorded from those subjects having a prominent 8- to 12-Hz tremor. In such subjects, the motor units producing 8- to 12-Hz activities were apparently more widespread in the extensor digitorum, as evidenced by the prominent 8- to 12-Hz bursts in the surface EMG (see, for example, Fig. 1). As mentioned previously, the 8- to 12-Hz sur-

face EMG modulation and tremor of two of our six subjects were quite minuscule, and recording 8- to 12-Hz-producing spike trains from these subjects was not accomplished, despite several attempts. Why some subjects exhibit widespread 8- to 12-Hz modulation of motor-unit activity while others do not remains unclear.

Because we have already demonstrated a strong correlation between the 8- to 12-Hz surface EMG modulation and 8- to 12-Hz tremor, sufficient evidence has been provided to conclude that the above motor-unit firing patterns underlie this tremor. To avoid any skepticism,

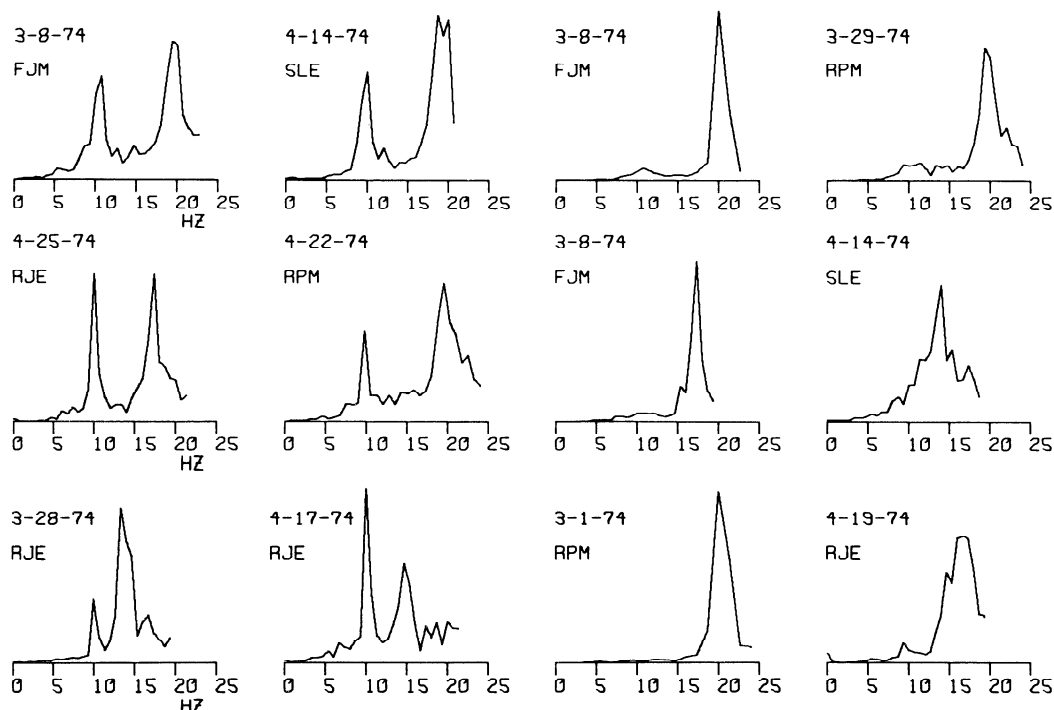


FIG. 4. Autospectra of 12 different motor units recorded from subjects *RJE*, *SLE*, *FJM*, and *RPM* during several experiments. Each spectrum was computed from 13 s of data, and the subject's initials and experiment data are shown with each spectrum.

we have included Fig. 5, in which the coherency spectrum for a simultaneously recorded spike train and tremor is shown. The motor unit in this figure had a mean firing frequency of 18.2 spikes/s and displayed the double-discharge pattern of firing. The 8- to 12-Hz activity produced by this motor unit was strongly coherent with the 8- to 12-Hz tremor (Fig. 5).

Simultaneous activities of contiguous motor units

It is clear at this point as to the types of individual motor-unit activities responsible for the 8- to 12-Hz finger tremor. It is also clear that the 8- to 12-Hz activities of individual motor units must have been synchronized to produce the gross amplitude modulation seen in the surface EMG. To directly demonstrate this synchronous behavior, we have performed phase and coherency analyses on six pairs of motor-unit spike trains, recorded simultaneously with the same electrode.

An example of this procedure is presented in Fig. 6, along with a portion of the needle electrode recording. The autospectra of two of the motor units obtained from this recording emphasize the important fact that, in general, the motor units did not fire at equal mean frequen-

cies. However, both motor unit *X* and motor unit *Y* produced 8- to 12-Hz spectral peaks, and coherency analysis disclosed a strong correlation between these two motor units in this frequency range, the coherency at all other frequencies being statistically insignificant.

Five of the six motor unit pairs produced a coherency spectrum like that of Fig. 6. The remaining pair contained a motor unit that did not have an 8- to 12-Hz spectral peak, and the coherency spectrum for this pair was statistically zero at all frequencies. The phase between the motor units of the five coherent pairs ranged from 0 to 37° at 8–12 Hz. However, additional motor-unit pairs should be tested to obtain an accurate distribution of phase values.

DISCUSSION

This study rigorously establishes an association between the 8- to 12-Hz component of finger tremor and an 8- to 12-Hz amplitude modulation in the extensor digitorum surface EMG. The individual motor-unit activity responsible for this amplitude modulation and tremor was not merely synchronized motor units firing at 8–12 spikes/s. Indeed, individual motor-unit spike trains with mean firing frequencies as high as 22 spikes/s produced 8- to

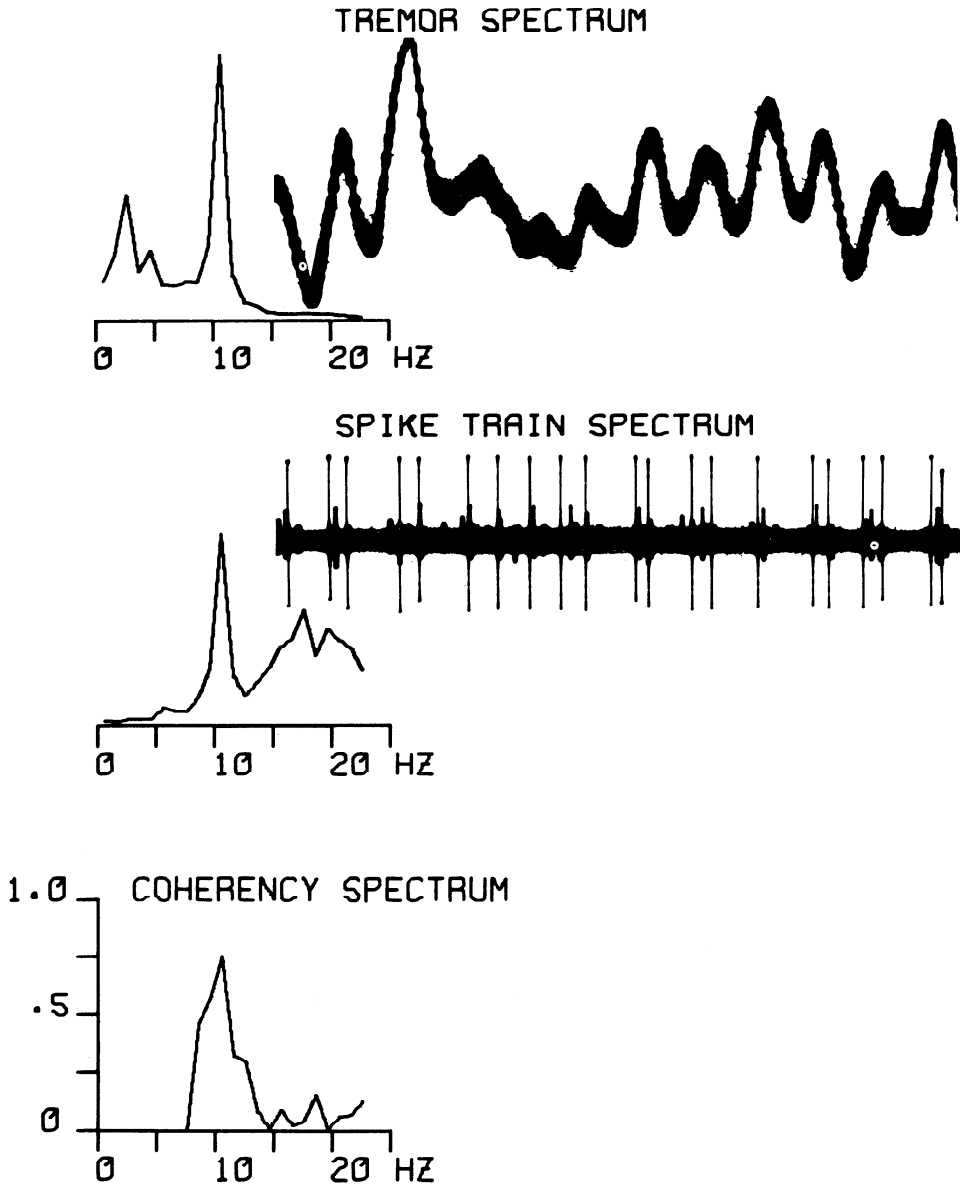


FIG. 5. Coherency analysis of simultaneously recorded finger tremor and motor-unit spike train (19 s of data). Sample 1-s records of the spike train and tremor are displayed with the corresponding spectra. Increased tension is a downward deflection in the tremor record. Each coherency value has 42 df, and coherencies greater than 0.13 are statistically significant at the 99% confidence level. Subject *RJE*.

12-Hz spectral peaks as a consequence of appropriately timed grouped discharges. Coherency analysis demonstrated that such motor-unit activity was responsible for the 8- to 12-Hz amplitude modulation in the surface EMG and for the 8- to 12-Hz component of finger tremor. Because 8- to 12-Hz activities were seen in individual motor units firing at 10–22 spikes/s, the 8- to 12-Hz “bursting” (amplitude modulation) in the surface EMGs could not have been a

random grouping of action potentials of asynchronous motor units firing at 8–12 spikes/s (40).

It should be emphasized that our study was limited to the extensor digitorum under the experimental conditions described. Therefore, we are not suggesting that all muscles exhibit the above motor-unit firing patterns during physiological tremor. Clearly, the large voluntary tensions (200–250 g) exerted by our subjects

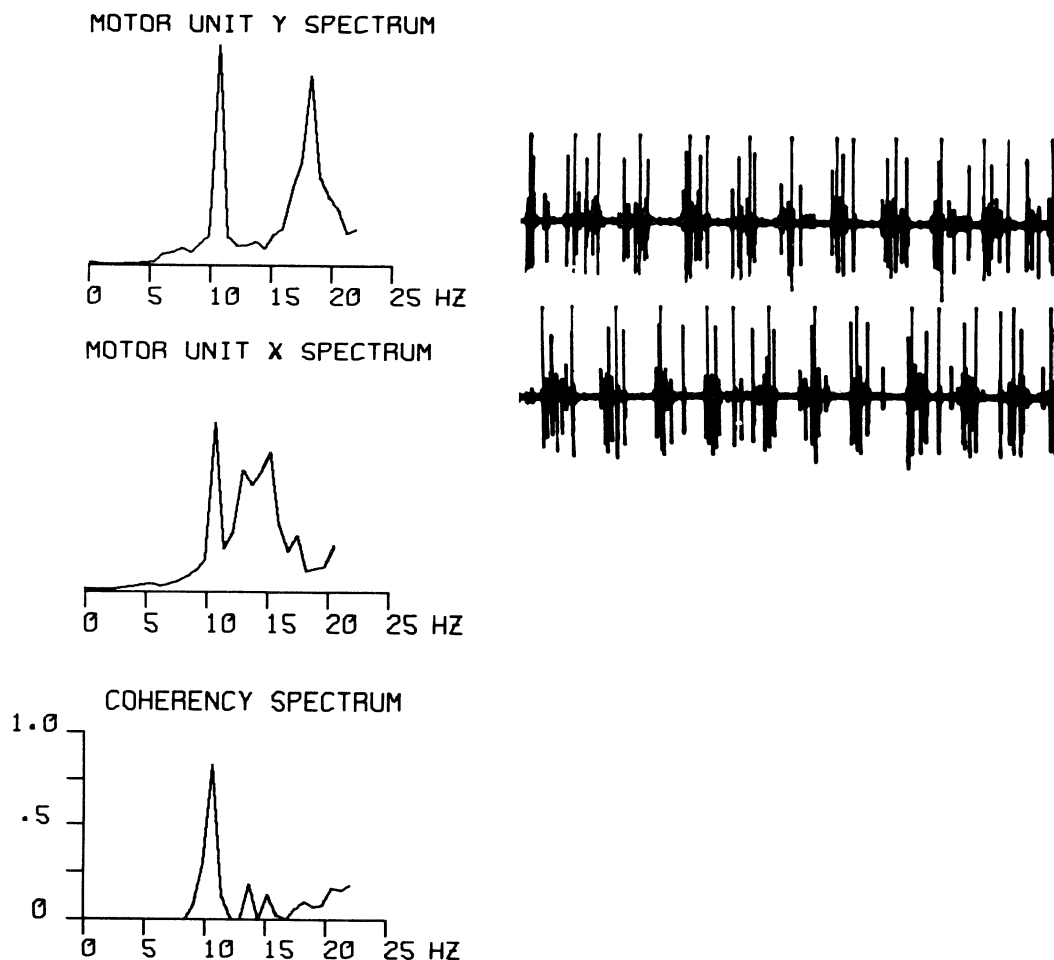


FIG. 6. Coherency analysis of two simultaneously recorded motor-unit spike trains (13 s of data). Shown with the spectra is an oscilloscope photograph of two consecutive sweeps of the needle electrode recording. Each sweep is 1 s in duration, and both sweeps give the visual impression of motor-unit synchronization. This impression is verified by coherency analysis of two motor units, *X* and *Y*, obtained from this data. Motor units *X* and *Y* had mean firing frequencies of 14.7 and 19.2 spikes/s, respectively, and the phase between these motor units at 11 Hz was $16 \pm 5^\circ$. Each coherency value has 26 df, and coherencies greater than 0.2 are statistically significant at the 99% confidence level. Subject *RJE*.

and the tendency for extensor digitorum motor units to fire at rates greater than 8–12 spikes/s (personal observation) are probably major reasons for the relative absence of motor units firing in the frequency range of the 8- to 12-Hz finger tremor. Furthermore, Mori (33) has conclusively demonstrated that human soleus motor units fire synchronously at 8–12 spikes/s in association with the 8- to 12-Hz tremor of this muscle.

In our experiments, the motor-unit spike trains that contained the greatest 8- to 12-Hz activities displayed a characteristic firing pattern in which transient periods of double discharges produced an 8- to 12-Hz rhythm. On

first recording these spike trains, it became apparent that the double discharges might consist of action potentials from two different motor units, despite the similarities in size and shape of the action potentials. However, we have ruled out this possibility on the basis of the following two tests.

First of all, we have followed several spike trains for over 70 consecutive seconds, observing over 1,400 consecutive action potentials and, despite the occurrence of numerous double discharges, never did we observe the two action potentials of such discharges to overlap. In fact, the shortest interspike interval observed was 8 ms. On the other hand, the action potentials of

two recognizably different motor units frequently overlapped, especially when they exhibited synchronous 8- to 12-Hz rhythms. Second, we have recorded the same spike train from different angles using a multipolar needle electrode, and the two spikes of the double discharges always had the same shape and amplitude, regardless of the electrode leads observed. Therefore, from these two lines of evidence, we conclude that the double discharges recorded in our experiments were truly produced by single motor units.

The mechanism of the 8- to 12-Hz component of finger tremor has been a source of considerable controversy (22, 24), but the stretch reflex has received the most attention (16, 18, 23). Specifically, Lippold et al. (23, 25) have proposed that the stretch reflex has a loop phase of -180° at 8–12 Hz, resulting in a tendency for this reflex to undergo oscillations (tremor) in this frequency range. The evidence for this "servo-loop" hypothesis is reviewed in a recent book (24), but several objections have never been satisfactorily answered (22).

Among these unanswered objections, two seem crucial. First of all, the mean frequency of the 8- to 12-Hz finger tremor clearly does not decrease on application of external mass loads to the extended finger (16, 23). In fact, all of our subjects exhibited an increase in frequency of approximately 1.0 Hz when masses of 200–500 g were suspended from the third digit.¹ In light of this fact, the servo-loop hypothesis requires that the mass of the third digit does not contribute additional phase lag to the stretch reflex, thereby making the frequency at which -180° loop phase occurs independent of mass loading. However, experimental support for this requirement is lacking, and at least two observations indicate that the frequency of stretch reflex-mediated oscillations should be a function of the mechanical properties of the moving anatomy (6, 41).

A second major objection to the servo-loop hypothesis has resulted from the observation that the mean frequencies of 8- to 12-Hz tremors in several muscles (12, 16, 22, 33, 37) are equal, regardless of the reflex arc lengths (22, 25). As an explanation for this observation, Lippold (24) has suggested that the delay inherent in the muscular response to motoneuron excitation is so great as to make the reflex arc

conduction time negligible. However, recent frequency analyses of human (32) and feline (26) skeletal muscles make this explanation untenable. For example, based on the frequency response of the human first dorsal interosseus muscle (32) and on a monosynaptic reflex conduction time of 23 ms (29), we estimate the muscle response delay at 8–12 Hz to be approximately twice the reflex arc conduction delay. Therefore, both delays are quite comparable in magnitude, and the resonant frequency of the stretch reflex should be a function of reflex arc length.

In light of the above two frequently raised objections to the servo-loop hypothesis, we wish to proffer an alternative hypothesis which we feel is far more consistent with previous tremor observations. Specifically, we suggest that Renshaw inhibition-rebound could well be the cause of the synchronous 8- to 12-Hz modulation in motoneuron firing observed in our experiments. Eccles and Hoff (11) and another group, Granit et al. (15), have demonstrated double discharges in tonically firing motoneurons of decerebrate cats in which the stretch reflex had been surgically interrupted, and the temporal characteristics reported for these double discharges are indistinguishable from those of our data. Furthermore, Granit et al. (15) have demonstrated that these double discharges are almost certainly a consequence of Renshaw (recurrent) inhibition and rebound excitation. Thus, as the excitatory drive to a motoneuron pool increases, the effect of recurrent inhibition gradually shifts from pure inhibition to inhibition-rebound excitation, resulting in double instead of single discharges (15). As a mechanism for this phenomenon, Granit et al. (15) proposed a rebound excitation following each transient period of Renshaw inhibition, with no additional interneurons involved.²

Therefore, as a mechanism for the 8- to 12-Hz finger tremor, we are essentially proposing the inhibitory phasing mechanism developed by Andersen and Andersson (1) for thalamic spindles. This mechanism explains why the tremor frequency is independent of both limb inertia and peripheral reflex arc length since, according to the inhibitory phasing theory, the temporal characteristics of recurrent inhibition-rebound determine the frequency at which a pool of neurons is synchronously mod-

¹ The 20- to 30-Hz component of finger tremor, seen when using an accelerometer for tremor measurement, has a mean frequency that is clearly determined by the mechanical properties of the extended digit. This "mechanical" component of finger tremor should not be confused with the 8- to 12-Hz component (38).

² The double discharges of this discussion should not be confused with those that arise from a delayed depolarization during the motoneuron action potential (7). The latter double discharges occur rarely during very moderate excitatory stimulation of the motoneuron and have temporal characteristics that are different from those reported in the RESULTS.

ulated. In this context it is worth noting that while the feline stretch reflex is extremely resistant to self oscillation at frequencies below 20 Hz (35), intercollicular decerebrate cats exhibit an 8- to 12-Hz clonus which may be a consequence of Renshaw inhibition-rebound and which has a mean frequency that is not affected by external mass loading (14).

In addition to explaining those observations which conflict with the servo-loop hypothesis, the recurrent inhibition-rebound hypothesis also explains a key observation which is thought to support the servo-loop hypothesis. In response to brief prods to the extended third digit, Lippold has observed 8- to 12-Hz finger oscillations and synchronous surface EMG bursts which were interpreted to be the result of forcing an underdamped stretch reflex (23). However, these oscillations and surface EMG bursts can also be explained on the basis of an excitatory volley to the motoneuron-Renshaw cell pool. Andersen and Andersson (1) have shown that an afferent volley to several thalamic nuclei produces a series of rhythmic discharges along the thalamocortical fibers as a result of inhibition-rebound, and the same phenomenon could be taking place in the motoneuron pool.

Although we propose recurrent inhibition-rebound to be the frequency-determining factor in tremor production, other factors, including the stretch reflex, may be responsible for determining the amplitude of tremor (27).³ Indeed, a stretch reflex of high gain would tend to sustain oscillations initiated in the Renshaw system by promoting synchronization directly through a common excitatory input to the motoneurons (31) and indirectly through inhibition-rebound (15). Such a supportive role for the stretch reflex could explain the conflicting observations concerning the effects of deaf-ferentation on tremor (17, 28). In fact, at least three studies indicate that spindle feedback may not be necessary for tremor production, although the absence of this feedback causes a profound decrease in tremor amplitude (2, 3, 22).

To our knowledge, only one observation has been made in previous studies which could be deemed an objection to our hypothesis. Lippold et al. (23, 25) have reported a lowering of the tremor frequency on cooling the limb in question. While such a maneuver undoubtedly slows the muscles in question and thereby increases the muscle component of the reflex delay, we

have repeatedly cooled the arm, forearm, and hand in ice baths at temperatures as low as 3°C for 60 min or more and have observed no significant change in the tremor frequency, despite both a drastic reduction in tremor amplitude and a pronounced slowing of the extensor digitorum twitch response to electrical stimulation (unpublished observations). Although negative results must always be regarded with caution, our failure to demonstrate an effect of temperature on the tremor frequency is supported by the work of Marsden et al. (27). Furthermore, Lippold et al. analyzed their tremor and EMG records visually, and it has been our experience that the reduction in tremor amplitude due to cooling is so great as to preclude objective visual analysis of tremor and EMG records, even in subjects that normally exhibit a large-amplitude tremor (see, for example, the tremor and EMG records of Lippold et al. in Figs. 6 and 10 of ref 23 and 25, respectively).

In closing, we submit that there is greater experimental precedent for the recurrent inhibition-rebound tremor hypothesis than for any other current hypothesis. Although the above discussion falls far short of settling the controversy which surrounds the 8- to 12-Hz finger tremor, we feel that careful consideration of our hypothesis in future experimentation will aid in resolving this interesting problem.

SUMMARY

Tremor of the extended third digit and bipolar surface and needle electromyograms of the extensor digitorum were recorded from six healthy volunteers for the purpose of elucidating the motor-unit activity responsible for the 8- to 12-Hz component of physiological finger tremor. Tremor was measured with a force transducer during steady voluntary contractions of approximately 200–250 g. The surface EMGs were full-wave rectified and low-pass filtered (–3 dB at 21 Hz), producing the envelope of the surface EMG (the demodulated EMG).

Spectral analyses of simultaneous tremor and demodulated EMG records were performed. In four of six subjects, a pronounced 8- to 12-Hz amplitude modulation in the surface EMG was present, and coherency analysis demonstrated that this modulation was strongly correlated with the well-known 8- to 12-Hz tremor. In two subjects this amplitude modulation and tremor were barely detectable, despite the sensitive recording and analysis techniques used in this study.

Spectral analysis was also performed on 43 motor-unit spike trains. Twenty-two spike trains, having mean firing frequencies in the

³ In using the unqualified term "tremor," we are referring to those 8- to 12-Hz tremors of various muscles (12, 25, 33, 37) which behave in a manner identical to that of the 8- to 12-Hz finger tremor.

range of 10–22 spikes/s, produced statistically significant spectral peaks at 8–12 Hz, in addition to the expected spectral peaks at the mean firing frequencies.

Of the 22 8- to 12-Hz-producing motor units, 12 had mean firing frequencies in the range of 17–22 spikes/s and exhibited the greatest 8- to 12-Hz activities of all motor units recorded. These motor units displayed transient sequences of double discharges in which interspike intervals (ISIs) of approximately 8–30 ms alternated with ISIs of 60–90 ms, thus producing an 8- to 12-Hz spectral peak. Adjacent ISIs of these motor units were correlated in the range of -0.5 to -0.9 . Coherency analyses demonstrated that the 8- to 12-Hz activities of these motor units were correlated with the 8- to 12-Hz finger tremor and surface EMG modulation.

The remaining 10 8- to 12-Hz-producing motor units had mean firing frequencies in the range of 10–17 spikes/s. Although these motor units did not display the intense double-discharge firing pattern of the more rapidly firing motor units, a tendency toward action potential grouping was present and resulted in 8- to 12-Hz spectral activities which were corre-

lated with the tremor and surface EMG modulation. Only 1 of these 10 motor units had a mean firing frequency in the range of 8–12 spikes/s.

Coherency analyses of six pairs of simultaneously recorded motor units revealed synchronization of the 8- to 12-Hz activities, despite differences in mean firing frequencies.

The 21 motor units that produced no spectral activity at 8–12 Hz fired more or less rhythmically with no grouping of motor-unit action potentials. This pattern of firing has been considered characteristic of tonic motor units during steady voluntary contractions.

The double-discharge firing pattern described in this paper is indistinguishable from that believed to be the result of Renshaw inhibition-rebound excitation. A tremor hypothesis is proposed which ascribes the frequency-determining factor in tremor production to Renshaw inhibition-rebound.

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