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Coherent modulations of human motor unit discharges during quasi-sinusoidal isometric muscle contractions

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Abstract

Spectral analysis of single-unit discharges, multi-unit EMG and muscle force during voluntary quasi-sinusoidal isometric contractions of two hand muscles revealed corresponding modulations of the firing rates of motor units at the frequency of the force oscillation. These rate modulations were correlated; and they showed a phase advance over the force oscillation, which is consistent with a cause-effect relationship between changes in firing rate and variations in force. These effects, observed over wide ranges of modulation amplitudes and frequencies, confirm the role of rate coding in the generation of time-varying muscle contractions; and they support the idea that during voluntary contraction of a given muscle, the motoneuron pool is subject to a common drive.

Key words: Human motor unit; Voluntary contraction; Sinusoidal isometric force; Interosseus muscle; Synchrony; Frequency analysis; Coherence

Information on the firing behavior of individual motor units (MUs) during time-varying muscle contractions is available mainly from studies of voluntary contractions in humans and locomotion in cats. For example, in humans, detailed analyses of the discharges of concurrently active MUs during quasi-static and slow ramp-like isometric muscle contractions have revealed correlatated variations of MU firing rates that resemble the variations of the muscle force [9,10]. Similarly, in cats, during locomotion, MU discharge rates show cyclic variations which closely parallel variations in the integrated EMG (e.g. [13]). These findings support the view that the alpha motoneuron pool is subject to a common drive.

The purpose of the present study was to systematically examine the firing properties of MUs and their role in the generation of muscle force in humans under more general dynamic conditions. In particular, we wished to know how the firing rates of MUs vary during voluntary muscle contractions of various strengths and speeds. To this end, single MU discharges and multi-unit EMG (wire and surface) were recorded from two hand muscles (the first dorsal interosseus, FDI, and the first palmar interosseus, FPI) during isometric contractions that varied quasi-sinusoidally. The sinusoidal forces had various amplitudes and frequencies covering much of the physiological range. Frequency-domain and time-domain analyses were used to examine the relationships between the discharge rates of MUs and the oscillations in muscle force. Two abstracts have been published [15,16].

Experiments were conducted on three healthy adults. Subjects exerted abduction forces (for FDI recordings) or adduction forces (for FPI recordings) with their index finger (lateral or medial sides of the proximal phalanx and interphalangeal joint) on a rigid annular cast attached to a strain gauge. They produced nearly-isometric forces that mimicked a set of target sine waves. The target sine wave serving as a template, was displayed on the oscilloscope and also presented to the subjects through earphones as a frequency modulated tone. These forces were about various mean force levels (up to 67% of maximum voluntary contraction, MVC); their amplitudes were in the range of 6–67% MVC and their

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frequencies in the range of 0.25–5.0 Hz. In addition, subjects produced steady isometric contractions at each mean level of force.

Single- and multi-unit activity in the FDI or the FPI muscle was recorded using bifilar nichrome wire electrodes (20 or 40μm, California fine wire Co.) inserted percutaneously into the muscle. Data was stored on magnetic tape, together with surface EMG and force, for off-line analysis. The EMG signal from the intramuscular wire was passed through a time-amplitude window discriminator (BAK Electronics) for isolation of single MUs. Discriminator pulses, multi-unit records and forces were sampled at 1 KHz. Multi-unit EMG signals were rectified and bin-integrated.

The recruitment threshold of an MU, determined using slow ramp-and-hold contractions, was defined as the lowest steady force level at which the unit fired continuously [11], and it was represented as a percentage of MVC. The mean level and amplitude of the target sine wave was adjusted so that the lowest force was above the unit's threshold and the highest force still allowed the unit to be discriminated.

Frequency analysis consisted of computations of auto-spectra of the various signals, and of coherence and phase functions for pairs of signals, using the Fast Fourier Transform (FFT [2]). The auto-spectrum exhibits the distribution of the average power (variance) of a signal as a function of frequency, and is particularly suited for identification and quantification of rhythmic components like the sinusoidal variations of this study. Coherence computations between single MU activities and muscle aggregate activity (EMG or force) can be used to assess synchrony (i.e. correlations) among active MUs [5–7,14]. The observation of a significant unit-to-population coherence at any given frequency implies the presence of correlations at that frequency between the particular unit and at least a fraction of other units in the population (the remaining uncorrelated units, acting like noise, tending to reduce the coherence).

Records were separated into segments in which the unit fired continuously for several cycles of the force oscillation (the minimum number for the 0.25 Hz sine wave was 2 cycles per segment). 15–30 such segments were analyzed for each frequency of the force oscillation. MU spike trains were represented as sequences of standard pulses. After mean and trend removal, each data array was windowed. It was then padded with zeros, to make its length equal to the nearest power of 2, and subjected to the FFT. For more details, see [14]. Auto- and cross-spectra were obtained as averages over the ensemble of data segments, and were used for coherence and phase computations. In the following account, spectral estimates of single- and multi-unit EMG are presented as relative power at each frequency.

Time-domain analysis included ensemble averages of consecutive cycles of force, multi-unit EMG and instantaneous MU firing rate, synchronized on the minima or the maxima of the force.

Fig. 1 (left column) shows the auto-spectra of three signals during quasi-sinusoidal abductions at 2.9 Hz: the discharges of a single MU, the surface EMG and the force.

The force spectrum consists of a single narrow peak near 2.9 Hz, indicating a nearly sinusoidal force signal. Similarly, the auto-spectrum of the surface EMG shows a dominant peak at the frequency of the force oscillation, and little additional power at higher frequencies. The auto-spectrum of the discharges of an isolated FDI unit has a clear modulating component at the same frequency as the force, reflecting a similar variation of the unit's firing rate (also see Fig. 2, top). In addition, this spectrum has a large peak at 11.5 Hz, the carrier frequency, and a smaller peak around the first harmonic of 11.5 Hz, both peaks representing the carrier signal (see [18], for examples of spectra of unmodulated and frequency-modulated spike trains). It should be noted that in a sinusoidally-modulated spike train the carrier frequency is equal to the mean rate of the spikes and this was confirmed for this unit by time-domain computations (see below).

The auto-spectrum of the unit's discharge during steady contraction at the same mean force level has no modulating component but shows a prominent peak near 12 Hz (Fig. 1, upper right), as well as smaller harmonic peaks, representing rhythmic MU firing at that frequency. Thus, the carrier rate of the modulated discharge was roughly the same as the mean discharge rate of the MU during steady muscle contraction at the same mean force level.

The unit-population coherences shown in the right column of Fig. 1 reveal the presence of significant correlations between the modulations of unitary activities at 2.9 Hz. (For the number of data segments used in this study, the 95% confidence interval for the coherence is around 0.1 [3,4]). The large, narrow peaks seen at 2.9 Hz in the coherences of unit to EMG (value, 0.54) and unit to force (value, 0.47) indicate that this unit's modulation was correlated to the modulations of a substantial fraction of the active MUs (see above).

In contrast, the very low unit-population coherences seen in these plots around the unit's carrier rate (11.5 Hz) indicate that the individual discharges of this MU were not significantly correlated with those of other MUs firing at neighboring rates.

Fig. 2 shows ensemble averages of consecutive cycles for the signals of the example of Fig. 1. Fluctuations in unitary firing rate can be seen to parallel sinusoidal variations in surface EMG and force and to have similar cycle periods. It is these variations that are reflected in the modulating components of the auto-spectra of Fig. 1. In addition, the oscillations present in the unit and surface records lead the force oscillation by 109 and 77

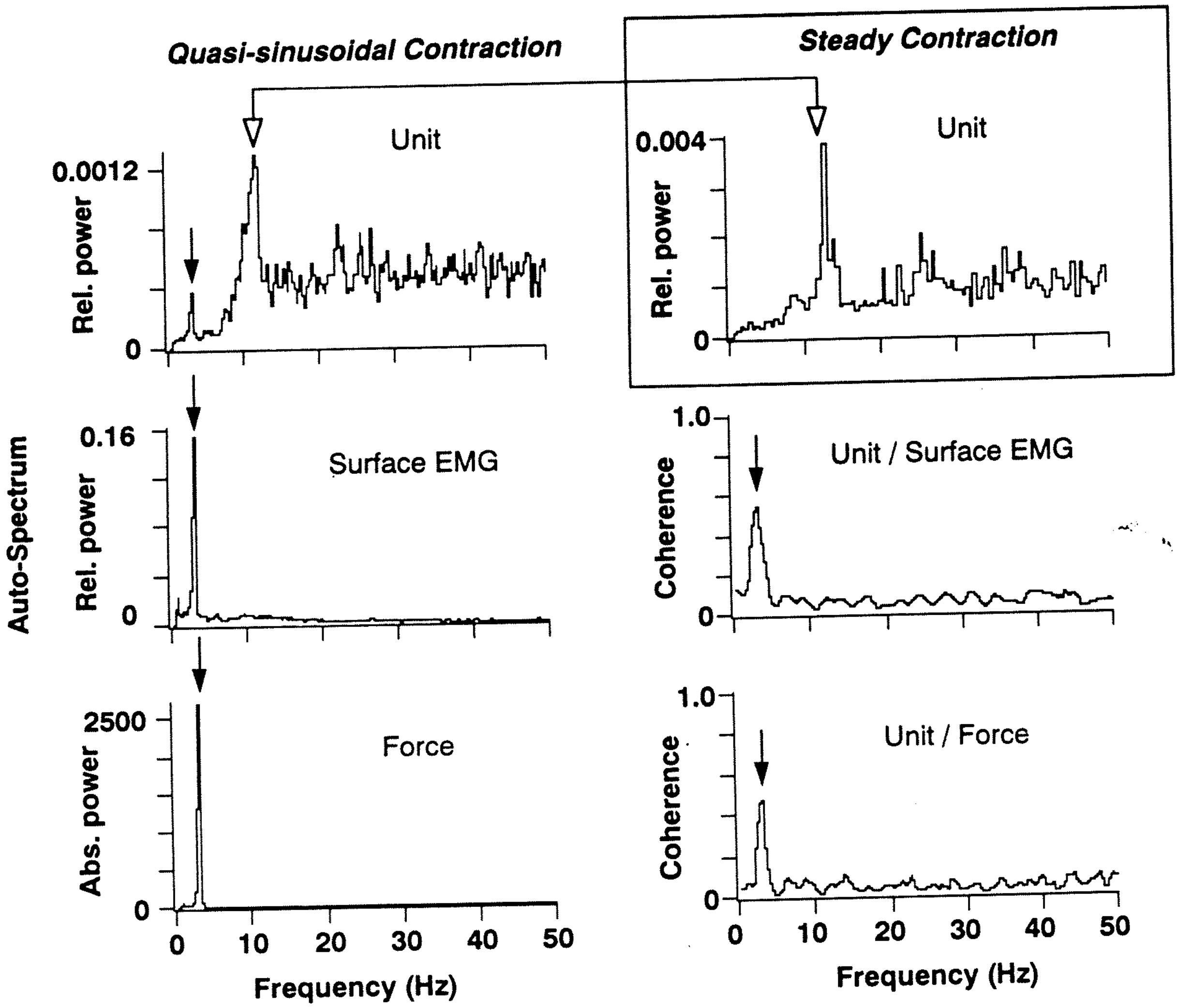

Fig. 1. Top row: auto-spectra of a MU's discharge during muscle force oscillation (left) and during steady muscle contraction at the same mean force level (right). The amplitude of the force oscillation (peak-to-peak) was 28% MVC and the mean force was 35.7% MVC. This MU was recruited at 20% MVC. Note the modulating component (2.9 Hz, light arrow) in left spectrum. Also note that the carrier component (11.5 Hz, dark arrow) in this spectrum is at about the same frequency as the peak reflecting the MU's rhythmic discharge during steady muscle contraction (11.5 Hz, filled arrow) in right spectrum. Middle row: Auto-spectrum of surface EMG over the FDI and coherence function between MU and surface EMG during force oscillation. Note large components at modulation frequency in both plots. Bottom row: Autospectrum for force and coherence between MU discharge and force.

ms respectively. This phase advance is in the range of times required for force to build up following electrical events in the muscle. Finally, the mean firing rate of the unit (dashed horizontal line) is 11.8 Hz, which is in good agreement with the carrier frequency identified in the unit auto-spectrum.

The following features, seen in the example illustrated in Figs. 1 and 2, were characteristic of our sample of 20 agonist units in FDI (18) and FPI (2).

1. The firing rates of MUs were modulated at the same frequency as the force. The power of the modulating spectral component, and hence the modulation depth, increased with both the amplitude and the frequency of the force oscillation. The increase in power with frequency could contribute to overcoming the well-known low-pass filtering properties of muscle [12,17].

2. For every MU and for all modulation frequencies and amplitudes studied, the carrier frequency was very close to the average firing rate of the unit (range 5–24 Hz) during steady contraction at the same mean force level.

3. Modulating components were present in multi-unit EMG spectra, and their relative power was much greater than that of the corresponding components for single MUs.

4. The modulations of the firing rates of MUs led the force modulation by 37–343 ms, and this phase advance generally decreased with increasing modulation frequency. The observed range of lead times is similar to that reported in [9] for reversals of activities during triangular contractions.

5. For all MUs, unit-to-population coherences showed

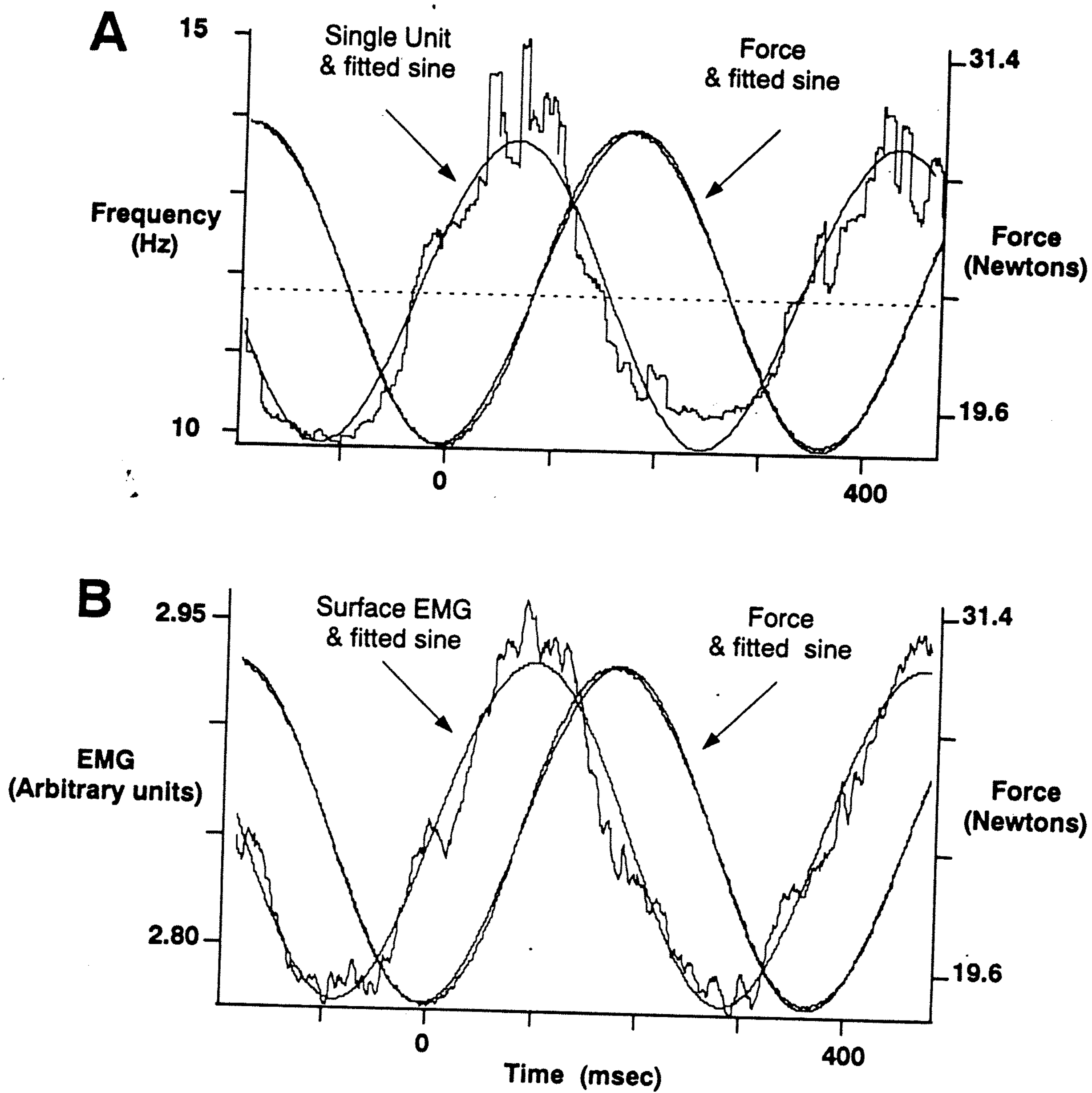

Fig. 2. Superimposed ensemble averages (n = 99) of force and MU firing rate (top) and of force and integrated surface EMG of FDI (bottom). Data synchronized on the force minima. Data are the same as those used in Fig. 1. Sine waves are fitted to the averages of the unit rate, muscle force and surface EMG signals. Note that variations in the average unit rate and surface EMG lead the force oscillation by 109 and 77 ms, respectively.

clear and significant peaks (range = 0.17–0.96) at the modulation frequency. In contrast, coherences were very low at other frequencies, including the carrier rates of the individual units.

Since none of the 20 units in our sample failed to show significant coherence to concurrently recorded population activities at the modulation frequency, it may be concluded that correlations between unitary modulations are widespread [6]. The correlations between the modulations of MU discharges described here should not be confused with correlations between individual MU spikes (e.g. [8]). The absence of significant coherences between single unit discharges and population activity at the units' carrier rates indicates that correlations between the spikes of different MUs are rare and weak. It is worth noting here the power of the unit-population coherence technique: from two readily recorded signals it provides information on unitary correlations at every frequency within the range of interest. In this case it has revealed the presence of correlations at the modulation frequency and their absence at the carrier frequencies of the MUs.

The finding of significant correlations between the modulating components of active MUs is consistent with the presence of a common time-varying drive to the motoneuron pool. This common input is likely to derive from supraspinal sources, since the frequencies and amplitudes of the force oscillations in this study were determined by volition. These observations confirm previous findings of other investigators [9,10,13] and extend them to contractions having a wide range of frequencies and amplitudes. It is plausible that the time-varying component of the descending drive to motoneurons causes the modulations of the firing rates of the MUs, while the mean level of this input determines their carrier rates.

Clearly, the degree to which unitary modulations are correlated should influence the amplitude of the resulting time-varying force. By varying the degree of synchrony, for example through changes in the number of interposed interneurons controlled by descending gating commands [1], the nervous system may have an additional mechanism for controlling dynamic forces.

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