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RESEARCH ARTICLE

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Frequency peaks of tremor, muscle vibration and electromyographic activity at 10 Hz, 20 Hz and 40 Hz during human finger muscle contraction may reflect rhythmicities of central neural firing

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Abstract The output from the central nervous system to muscles may be rhythmic in nature. Previous recordings investigating peripheral manifestations of such rhythmic activity are conflicting. This study attempts to resolve these conflicts by employing a novel arrangement to measure and correlate rhythms in tremor, electromyographic (EMG) activity and muscle vibration sounds during steady index finger abduction. An elastic attachment of the index finger to a strain gauge allowed a strong but relatively unfixed abducting contraction of the first dorsal interosseous (1DI). An accelerometer attached to the end of the finger recorded tremor, surface electrodes over 1DI recorded EMG signals and a heart-sounds monitor placed over 1DI recorded vibration. This arrangement enabled maintenance of a constant overall muscle contraction strength while still allowing measurement of the occurrence of tremulous movements of the finger. Ten normal subjects were studied with the index finger first extended at rest and then contracting 1DI to abduct the index finger against three different steady forces up to 50% of maximal voluntary contraction (MVC). Power spectral analysis of tremor, EMG activity and muscle vibration signals each revealed three frequency peaks occurring together at around 10 Hz, 20 Hz and 40 Hz. Coherence analysis showed that the same three peaks were present in the three signals. Phase analysis indicated a fixed time lag of tremor behind EMG of around 6.5 ms. This is compared with previous measurements of electromechanical delay. Other experiments indicated that the three peaks were of central nervous origin. Introducing mechanical perturbations or extra loading to the finger and making recordings under partial anaesthesia of the hand and forearm demonstrated preservation of all the peaks, suggesting that they did not originate from mechanical resonances or peripheral feedback loop resonances. It is concluded that, at least for a small hand muscle, there exist not one but a number of separate peak frequencies of oscillation during active contraction, and that these oscillations reflect synchronization of motor units at frequencies determined within the central nervous system. It is proposed that the multiple oscillations may be a means of frequency coding of motor commands.

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Introduction

The concept that the output from the central nervous system (CNS) controlling muscle activity is rhythmic in nature was first introduced by Adrian and Moruzzi (1939). Their idea arose from recordings of pyramidal tract and motor cortical discharges in anaesthetised animals. Recent monkey studies have shown synchronized discharges of corticomotoneurones at certain frequencies (Murthy and Fetz 1992; Nicolelis et al. 1995), suggesting a common rhythmicity. However, detailed analysis of these rhythms in man is difficult because of the relative inaccessibility of the human brain to recording techniques and problems with correlating poorly localized cortical activity with particular motor tasks. One approach to the problem is to focus directly on the motor output, looking for any manifestation of central rhythmic activity at the peripheral level. Oscillations in the motor cortex that modulate descending corticospinal pathways might result in a similar pattern of modulation of muscle electromyographic (EMG) activity and of movement in the form of a tremulous oscillation.

A great deal of work has already been carried out on peripheral oscillations (see reviews by Marsden, 1978, and Freund, 1983). Three main techniques have been employed in humans, namely those involving EMG recordings, muscle vibration recordings and movement (tremor) recordings (Table 1).

Peak frequencies of oscillation occurring in EMG signals have been recognized since Piper's (1907) descrip-

Table 1 Summary of reports on peak EMG, muscle vibration and tremor frequencies in distal limb of healthy subjects

Reference	Location	Condition	Frequency (Hz)	Proposed origin
Peak EMG frequency				
Piper (1907)	Large muscles	Strong contraction	ca. 50	Synchronization of motor units
Adrian (1925)	Different muscles	Strong contraction	35–60	Mechanical resonances
Fex and Krakau (1957)	Different muscles	Contraction	ca. 50	Active motor unit synchronization
Elble and Randall (1976)	Finger	Isometric contraction	8–12, 13–22	Lower frequency is synchronized
Hagbarth et al. (1983)	Different muscles	Steady voluntary contraction	ca. 50 (Piper rhythm) + single units at subharmonics	Synchronization by CNS rhythms
Homberg et al. (1986)	Finger and arm muscles	Isometric contraction (+ force tremor)	8–10 (finger), 8–20 (arm)	Motor unit firing
Farmer et al. (1993a, b)	1DI	Correlation between single motor units on weak contraction	1–12, 18–32	Mechanical and CNS, respectively
Muscle vibration frequency				
Wollaston (1810) in Orizio 1993	Muscle belly	Contraction	ca. 20–30	Muscle fibre activity
Gordon and Holbourn (1948)	Single motor units	Contraction	25–30	Mechanical “spikes” from unit firing
Oster and Jaffe (1980)	Different muscles	Isometric contraction	25	Actomyosin cross-linking dynamics
Keidel and Keidel (1989)	Masseter, biceps, wrist extensors, tibialis anterior	At rest and isometric contraction	At rest, multiple peaks ca.10. On activity, also 20–100	Motor unit firing. Peaks due to unit synchronization.
Gamet and Maton (1989)	Biceps brachii	Fatiguing isometric contractions	10–16	Motor unit firing
Orizio et al. (1990)	Biceps brachii	Strong isometric contraction	5–10 + 10–20	Firing rates of slow and fast motor units
Tremor frequency				
Horsley and Schafer (1886)	Different muscles	Electrically induced contraction	10	Property of muscle
Halliday and Redfearn (1956)	Finger	On posture and loaded	10	Stretch reflex loops
Stiles and Randall (1967)	Finger	Mechanical perturbation	25–30	Mechanical resonance
Sutton and Sykes (1967)	Hand	Steady forceful contraction	9	Visually dependent
Dymott and Merton (1968)	Hand	Steady forceful contraction	9	Visual and non-visual components
Marsden et al. (1969a, 1969b)	Fingers/hand	On posture	9	Multifactorial (CNS component)
Elble and Randall (1976)	Finger force tremor	Isometric contraction	8–12	Synchronization of motor units by Renshaw cell activity
Allum et al. (1978)	Small hand muscles	Isometric contraction	6–12	Overlap of slow corrective fluctuations and motor unit firing
Hagbarth and Young (1979)	Hand/forearm	Spindle afferents on tremulous contraction	8–10	Stretch reflex loops
Lakie et al. (1986)	Hand	On posture	9	Mechanical
Sakamoto et al. (1992)	Fingers	On posture	10, 25	Peripheral feedback
Vallbo and Wessberg (1993)	Finger (+ surface EMG recording)	Slow movement	8–12	CNS
Amjad et al. (1994)	Finger	On posture	10, 30–40	10 = mechanical 30–40 = CNS

tion of rhythmical bursts of EMG signals at around 50 Hz while recording from steadily contracting muscle using surface electrodes and a string galvanometer. Findings of peaks of oscillatory EMG activity in a similar broad frequency range of 40–70 Hz have been confirmed by many studies on different muscles under different conditions (Adrian 1925; Fex and Krakau 1957; Komi and Viitasalo 1975; Hagbarth et al. 1983; Bruce and Ackerson 1986). Adrian (1925) suggested that the origin of EMG synchronization at the Piper frequency could lie in mechanical resonance at this frequency producing afferent responses entraining the EMG at the same frequency via reflex action. However, microneurographic recording of afferent nerves has revealed no such rhythmic behaviour correlated with EMG Piper rhythms (Hagbarth et al. 1983), suggesting that the rhythms are centrally driven. Piper rhythm frequencies have not been found in studies correlating activity between single motor units. These have instead revealed a central EMG modulation in a much lower frequency range from 18 to 29 Hz (Farmer et al. 1993b). Other reports describe EMG oscillations only in the 8- to 12-Hz range. Some consider these oscillations merely to reflect minimum or modal firing frequencies of individual motor units (Allum et al. 1978; Homberg et al. 1986) or linked motor units (Dietz et al. 1976), while others demonstrate a clear power spectral peak due to synchronization of motor units driven together at this frequency (Mori 1975; Elble and Randall 1976; Elble 1986).

Since muscle contraction is triggered by EMG activity, peak frequencies of oscillation in the EMG should be associated with similar frequency peaks in muscle vibrations. However, the literature reveals a confusing variety of peak values that poorly match with EMG rhythms. The first description of an investigation of muscle vibrations dates back to 1665, when Grimaldi listened for these vibrations propagated as sound waves. Oster and Jaffe (1980) quantitatively investigated muscle vibrations during contraction using a transistorized stethoscope and found a frequency peak of sound vibration at 25 Hz; this peak frequency was unaffected by the sound transmission medium and by loading of the muscle. Microphones and accelerometers have since been used to record vibrations from contracting muscles. Those that describe any peak frequencies find them to be variable and generally confined to the 10-Hz range (Rhatigan et al. 1986; Gamet and Maton 1989; Wee and Ashley 1989; Rouse and Baxendale 1993; Ebrahimi-Takamjani and Baxendale 1994). However, Orizio et al. (1990) also describe a higher frequency range, from 10 to 20 Hz, which they ascribed to firing of a fast motor-unit population, while Keidel and Keidel (1989) report additional activity in a variety of strongly contracting muscles in a broad range from 20 to 100 Hz.

Finally, many recordings of the oscillation of a body part (so-called physiological tremor) have been carried out. A peak oscillation frequency of the finger, hand or forearm is usually found at around 10 Hz at rest (Yap and Boshes 1967; attributed to the ballistocardiogram), on posture (Halliday and Redfearn 1956; Marsden et al. 1969a; Lakie et al. 1986), while loaded (Halliday and Redfearn 1956; Joyce and Rack 1974; Homberg et al. 1986), during slow free finger movements (Vallbo and Wessberg 1993) and in force fluctuations during isometric contraction (Dymott and Merton 1968; Sutton and Sykes 1967; Homberg et al. 1986; Reitsma 1994). Higher frequency tremors are occasionally reported. Stiles and Randall (1967) found that introducing sudden finger perturbations resulted in 25–30-Hz oscillations that were considered to represent resonance at the mechanical fundamental frequency. Sakamoto et al. (1992) and Amjad et al. (1994) found a postural finger tremor at a similar frequency. However, the first of these reports suggested this peak was due to stretch reflex resonance, while the other considered a CNS oscillator to be the origin.

It is clear that there is considerable confusion between studies on peripheral oscillations, both with respect to the frequencies of importance and their origin (Table 1). Any neuronally mediated oscillation should be found in EMG, muscle vibration and tremor. Such a corrrespondence is not apparent on reviewing the literature. Some studies have successfully demonstrated correspondence between EMG and tremor (Elble and Randall 1976; Matthews and Muir 1980; Elble 1986; Homberg et al. 1986) and between EMG and muscle vibration (Orizio et al. 1990) at 10 Hz but not at the higher frequencies. Even at 10 Hz, it is not clear whether this component of tremor merely reflects the most common firing frequency of individual units, whether the tremor drives the EMG by reafference or whether both signals reflect a synchronization of motor units by peripheral feedback loop resonance or by a central oscillator.

The present study addresses these issues by employing a novel method that enables simultaneous measurement of finger oscillations by all three techniques (EMG, muscle vibration and tremor). Previous studies of oscillations at rest or on posture are handicapped by the lack of clearly defined and measurable muscle activity and by the danger of contaminating oscillations from other sources. Some workers have solved such problems by using inertial loads or by using a rigid fixation and measuring isometric contraction. However, tremor oscillations are now either completely abolished or severely dampened and shifted to low frequencies (Homberg et al. 1986). The present study measures contraction against an elastic resistance. This allows a strong contraction suitable for EMG and muscle vibration recording in active conditions, yet also an unrestricted tremor oscillation. Elastic resistances raise the mechanical resonance frequency of the arrangement, which has the additional advantage of facilitating detection of higher frequency tremors and allows the mechanical resonance frequency to be clearly identified and separated from neuronally mediated oscillations. The mechanical effect of elastic loads has previously been described by Joyce and Rack (1974) and Matthews and Muir (1980), who investigated upper arm contractions against a spring to distinguish mechanical tremor from peripheral feedback loop resonance.

Analysis of contractions of 1DI against elastic resistances in this study reveals a much wider range of tremor oscillations than heretofore described. Not one but three peak oscillation frequencies are present, occurring at around 10 Hz, 20 Hz and 40 Hz. Furthermore, each of the three peaks is also clearly demonstrated in the EMG and muscle vibration records. Thus the long-described, 40-Hz-range Piper EMG rhythm is now shown in muscle vibration and tremor. We also present evidence indicating that the peak frequencies represent synchronized activity of numbers of motor units entrained by oscillators in the CNS. Similar studies of peripheral oscillations may therefore prove a valid and fruitful means of investigation of CNS oscillators and their role in controlling motor activity.

Materials and methods

The experiments were performed on ten normal, right-handed volunteers whose ages ranged from 27 to 45 years. Informed consent was obtained from each subject and the study was performed with local Ethical Committee approval.

Equipment and setup

Abduction of the right index finger caused by contraction of 1DI was studied (Fig. 1). The subject was seated comfortably with the forearm and hand resting in a pronated position on a rigid horizontal table. The arm was supported and stabilized from the elbow to the metacarpophalangeal (MCP) joints on the ulnar side to allow forceful abduction at the 2nd MCP joint to occur with freedom, but without necessitating co-contraction of muscles other than 1DI. This was confirmed by demonstrating surface EMG silence in the forearm muscles.

Voluntary, steady abduction of the index finger was made against an elastic band (stiffness around 30 N/m) attached to the distal phalanx. The other end of the elastic was connected to a strain gauge, which registered the force of contraction. The strain gauge assembly consisted of a piezo-electric wire strip applied along a heavy metal bar that was arranged parallel to the hand free at one end and fixed at the other. The magnitude of the tremulous movement at the end of the finger was very small (<1%) compared with the degree of stretch of the elastic, so that the force exerted against the elastic would change only negligibly at different phases of the tremor. Different strengths of steady contraction could be studied by changing the position of the limb supports to alter the length of the elastic. During recordings, the subject held the index finger parallel to the arm and raised slightly off the table. The interphalangeal joints were kept extended but not forcibly so.

In the main experiment, the tremor of the index finger occurring during the steady contraction was measured by a miniature piezo-resistive accelerometer (Vibro-Meter SA105; Fribourg, Switzerland) taped firmly to the end of the finger so that its direction of detection corresponded to an abducting-adducting movement. The accelerometer weighed 6 g and had a linear range of acceleration response up to 200 ms^{-2} and a linear frequency response range of 0–200 Hz. The accelerometer was insensitive to movement vectors in other directions. Surface EMG of 1DI was recorded by two 9-mm-diameter silver/silver chloride electrodes placed on the muscle belly and over the proximal phalanx.

Two techniques were employed to obtain records of muscle vibration frequencies (termed the acoustomyogram, AMG). First, an electronic transistor stethoscope (Bosch-EST 40, Berlin, Germany), with a frequency response up to 250 Hz, was used both to listen to the sounds of 1DI contraction and to record the electronic signal to obtain a power spectrum of the vibrations. The 1-cm-diameter hemispherical recording area of the stethoscope was clamped in firm contact with the muscle belly of 1DI so that the signal could both be listened to via the ear piece attachment and could be amplified and recorded in the same way as the accelerometer signal. Second, an accelerometer was attached to the muscle belly of 1DI instead of its usual attachment site at the end of the finger. By these means, a direct recording of muscle vibration would be made rather than tremor transmitted along the finger. The direction of detection of acceleration was perpendicular to the skin surface. EMG records could not be taken at this time. This arrangement was also used to record a true isometric contraction by using a fixed rather than elastic attachment to the finger.

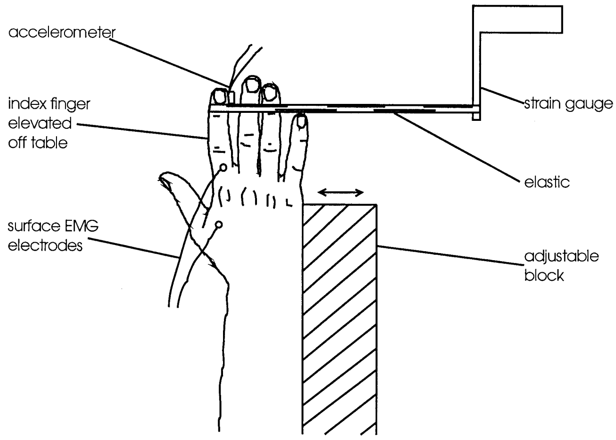


Fig. 1 Plan of experimental arrangement

Recordings

The d.c. accelerometer and strain gauge signals (measuring tremor and force respectively) were amplified and digitized with 12-bit resolution by a 1401-plus (CED, Cambridge, UK) analogue-to-digital converter. Recordings were sampled at 2008 Hz in those experiments conducted to determine the frequency bands of interest and whenever analysis of the EMG or AMG frequency bands was to be performed. When tremor frequencies alone were being analysed, the sampling rate was reduced to 333 Hz. The EMG signal was amplified by a Digitimer D 180 (Welwyn, UK) amplifier and filtered with a low-pass multi-stage filter set at 1 kHz to ensure that no frequencies would be present above the Nyquist frequency for Fourier analysis. A high-pass filter was set with a 3-ms time constant to prevent artefactual frequencies due to electrode movement from appearing in the EMG records. The EMG was digitally sampled at 2008 Hz and digitally full-wave rectified. The signals were displayed and stored on computer disk by a software package (CED Spike 2) running on an IBM PC microcomputer. A separate microcomputer ran a program that simultaneously triggered a recording period when the subject was ready and gave the subject a visual display indicating the start and end times of the recording period.

Protocol

The MVC strength of the subject was first determined by using an inelastic attachment to the strain gauge and recording the greatest signal obtained during three brief maximal abductions of the index finger.

To avoid fatigue (which was found to have a deleterious effect on the results), recordings were made over periods of 6.2 s. At all times during the recording, the subject looked at the visual display, which indicated when a recording was in progress. He was instructed not to look at the finger because of the known tremor frequency peaks that are visually dependent (Merton et al. 1967; Sutton and Sykes 1967). A full trial consisted of ten recording periods with adequate rests of at least 15 s between each period. When tremor and EMG or AMG were recorded simultaneously, up to 20 periods at 50% MVC strength were recorded.

Trials at four different contraction strengths were conducted; at “rest” (defined as silent 1DI EMG) and at 12.5%, 25% and 50% of MVC. They were generally performed in increasing order of contraction strength, although the results were no different when the order was reversed. The subject was encouraged to relax all muscles other than 1DI and was instructed not to allow any other parts of the body to touch the index finger, the elastic attachment or the limb supports. All other potential extraneous vibrations were similarly minimized. If the subject reported fatigue, the trial was terminated. MVC was remeasured after the experiment to confirm a lack of fatigue. A constant force contraction was easily maintained by keeping the finger approximately stationary during contraction. No major fluctuations were observed in the strain gauge force records.

Analysis

Raw records were examined for periodic tremor activity and regularities in rectified EMG activity (Fig. 2). The main analysis consisted of power spectral estimates of the accelerometer, AMG and EMG records of each trial. This was done by finite fast Fourier transformation (FFT) using a commercial software package (CED Spike 2). The block size for analysis was set at 2048 points, which gave a bin width of approximately 1 Hz. In each trial, averaged power spectral estimates were derived from up to 120 contiguous FFT data blocks. After initial inspection, the averaged spectra were displayed with a magnified frequency scale, since the regions of interest were at the lower end of the spectrum. (For isolated analysis of tremor records sampled at 333 Hz, the block size was 512 points, giving a bin width of 0.65 Hz and summation over 40 FFT blocks). Artefacts in analysis resulting from the non-cycling nature of the data blocks were dealt with by the standard technique of applying a raised cosine window to each FFT block (Hanning) and compensating for the resultant loss of power. This procedure results in a high level of power in the first two frequency bins, but the frequencies of interest are well outside this range. Since the level of contraction was approximately constant, local stationarity of the acceleration signal could be assumed. The *y*-axis of the spectral plots was mean-square power, equivalent to the variance of signal amplitude (i.e. a “square of signal amplitude” parameter). For acceleration data, this was converted into units of the square of acceleration of the finger. The accelerometer could be calibrated by recording the signal change when rotated 90° on its long axis; this would equal acceleration due to gravity (*g*), which was converted into units of centimetres per second squared.

Coherence analysis was performed between the tremor (accelerometer) data and the EMG data to check for a match between the frequency peaks in their respective power spectra (Jenkins and Watts 1968). An upper 95% confidence line was calculated based on the mean and standard deviation of the coherence values of the whole spectrum. (This method was chosen to indicate when peaks in coherence were significantly greater than the background level. Coherence per se was always significantly greater than zero, as expected for a movement and an EMG measure of the same activity, as illustrated by the 95% confidence threshold for non-zero coherence determined by the standard method; Farmer et al. 1993b). The phase differences between the coherent frequencies were determined by a separate program running in the Spike2 environment, which calculated the difference between the arctangents of the ratios of the imaginary and real components of the Fourier transform at each frequency (J. McAuley, unpublished work).

To corroborate the findings of the tremor frequency peaks, interval analysis of the tremor records was performed in the time domain. In this experiment, the accelerometer record was high-pass filtered with a time constant of 300 ms so that slow d.c. shifts would be eliminated. Individual peaks in the tremor record were recorded on-line by means of a Schmitt trigger sending a digital transistor-transistor logic (TTL) pulse whenever the tremor acceleration crossed above a certain threshold determined after a preliminary examination of the filtered tremor signal.

Other experiments

On three subjects, after each trial at a certain contraction strength, the trial was repeated with the single difference that the finger-elastic-strain gauge arrangement was intermittently plucked/tapped sharply by the experimenter in order to bring out the mechanical resonance frequencies of the apparatus and finger at that level of tension. The perturbations were small enough not to interfere with the subjects’ performance of the task but were large enough to produce their own frequency peak. They were performed irregularly at intervals of 1–3 s.

To determine whether the origin of the frequency peaks was central or derived from peripheral feedback, the experiment was repeated with the limb anaesthetised by a cuff applied around the upper arm and set well above arterial pressure. A time window was available when the ischaemia resulted in total lack of deep and superficial sensation but still enough muscle power to perform the experiment. On sudden release of the cuff, there was also a brief period where muscle power had returned while sensation was still absent. As well as by ischaemia, anaesthetic conditions were also created by ulnar nerve block with an infusion of 4 ml of 2% lignocaine around the nerve at the elbow. The role of peripheral feedback and mechanical resonances was further investigated by recording the EMG, AMG and tremor during similar elastic contractions in three subjects while the end of the finger was loaded by wrapping lead strips around it. The weights varied from 20 to 140 g.

Results

Tremor, EMG and force traces

Observation of traces in all the subjects studied revealed that the tremor and EMG bursts were not random but often consisted of cycles of regular wavelength. For example, Fig. 2A shows periods of 25-ms cycling and 50-ms cycling in both the EMG and tremor (accelerometer) recordings. This impression was confirmed by triggering a digital event off the peaks in the tremor signal and plotting an interval histogram of their distribution in time (Fig. 2B). The variability in the record meant that only a proportion of the peaks were correctly triggered and that some noise events were falsely triggered, but it was still clear that there were three separate peak intervals at about 25 ms, 50 ms and possibly 110 ms, but not at 75 ms. These correspond to oscillations at 40 Hz, 20 Hz and 9 Hz.

The amplitude of the oscillations was determined from calibration of the accelerometer as described in Materials and methods. Maximum peak-to-peak accelerations of 40-Hz oscillations observed in the 50% MVC traces were about 9 ms^{-2} and about 5 ms^{-2} for 10-Hz oscillations. (This equated to displacements of 0.15 mm at 40 Hz and 1.2 mm at 10 Hz; the total stretch on the elastic beyond resting length was always at least 100 mm.) The force corresponding to the maximum acceleration, using an estimate for the mass of the finger (40 g) and given that the finger is pivoted rather than free, was determined to be around 120 mN. This should not be compared with single-unit force values obtained by spike-triggered averaging techniques (Desmedt and Godaux 1977), since these studies assume a priori that no synchronization occurs between units. In the thenar muscle, the mean and SD of twitch forces developed by a single motor unit triggered by intraneural axon stimulation at 10 Hz was found to be only 9±7 mN, with a maximum value of 25 mN (Thomas et al. 1990). This value would be even smaller at higher firing frequencies because of progressively greater fusion of twitches. The mechanical advantage through which this muscle acts is not likely to be much poorer than that for 1DI and the distances from the pivot to the point of measurement of force or acceleration are comparable. It therefore appears that in the present study a number of units must have been acting together to generate the observed oscillations.

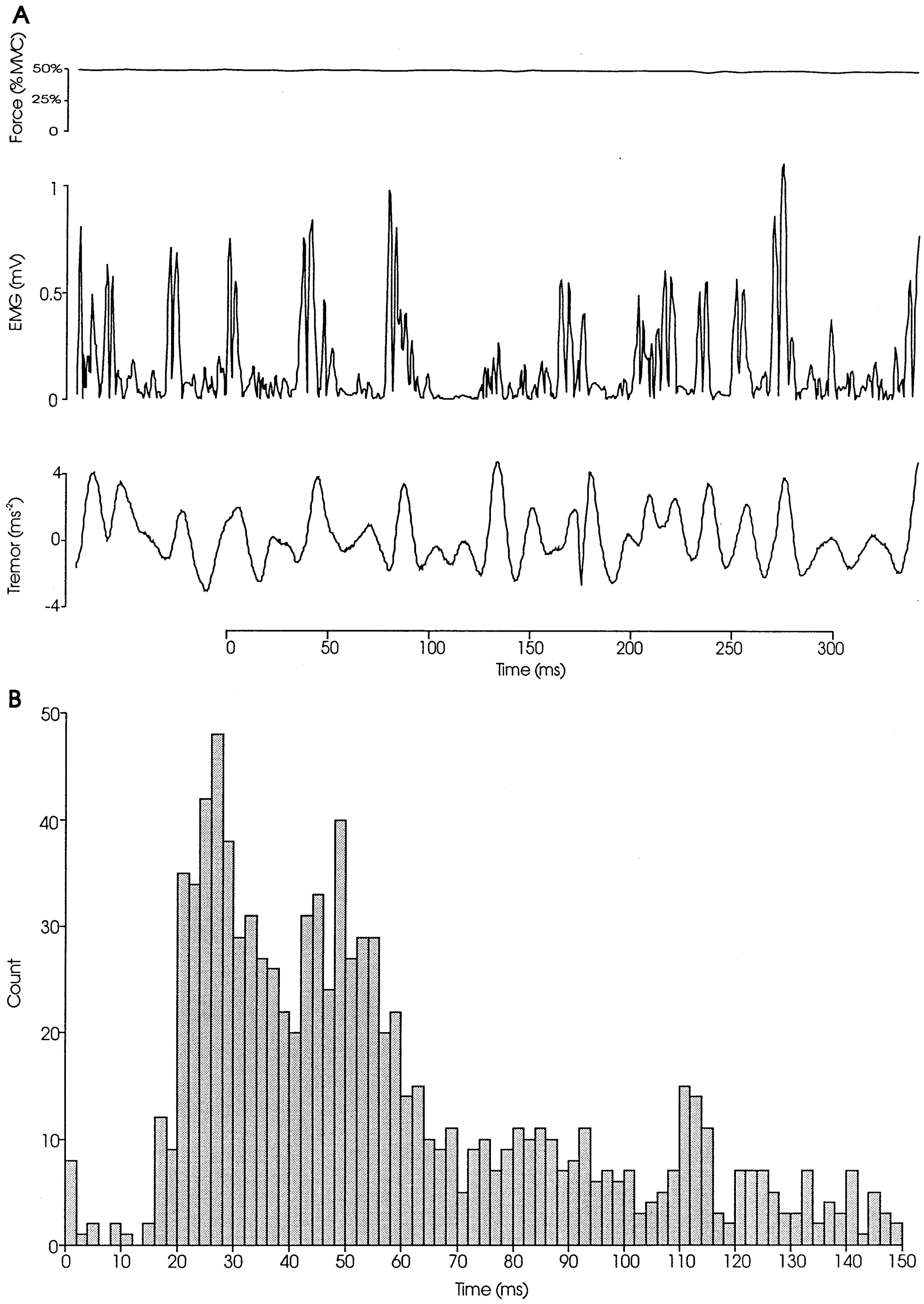


Fig. 2 **A** Force, EMG and tremor during a 50% maximum voluntary contraction (*MVC*) of the index finger abducting at the metacarpophalangeal joint against an elastic load. The *top trace* indicates the relatively stable force level as measured by a strain gauge. The *middle trace* is a rectified surface EMG recording from the first dorsal interosseous muscle and shows bursts of activity initially at approximately 50-ms intervals and, in the second half of the record, at about 25-ms intervals. The *bottom trace* is an accelerometer recording of horizontal acceleration at the end of the finger, upward deflection corresponding to the abducting direction. The oscillations in the acceleration (tremor) record show activity clearly associated with the EMG bursts. **B** Interval histogram of peaks of tremor oscillation as measured by the accelerometer during 50% MVC against an elastic load. The events for the histogram are derived by on-line triggering off the positive acceleration deflections in the tremor trace. The trigger level was here set at $+1\ ms^{-2}$. Clear peaks are present at 25 ms and 50 ms and less clearly at 110 ms. The 25-ms peak indicates that there is a genuine cycling at 40 Hz occurring over the whole recording

The activity in the EMG record generally occurred as polyphasic bursts in the same regular rhythm as in the corresponding tremor trace (Fig. 2A). Even when bursts appeared rather simple in form and brief in duration, their unrectified surface EMG peak-to-peak amplitudes were generally over 2 mV, suggesting that they were really multi-unit rather than single-unit discharges. The polyphasic nature was confirmed by some concomitant needle EMG recordings. Thus both the nature of the EMG bursts and the magnitudes of the corresponding force fluctuations indicate that the oscillations were produced by groups of synchronized units.

Power spectra and coherence

Power spectral estimates of the whole traces during active contraction confirmed the initial impression of the occurrence of regular rhythms at certain frequencies. The power spectrum reflects the power or magnitude of oscillation (variance) of the signal at different frequencies over the full duration of the recording. The most striking finding was the clear presence of not one but three peaks in frequency of oscillation in both the tremor (Figs. 3, 4) and EMG (Fig. 4) signals. Although the peak frequency values varied somewhat from trial to trial and from subject to subject, they fell within three discrete frequency bands centred at around 10 Hz, 20 Hz and 40 Hz. These

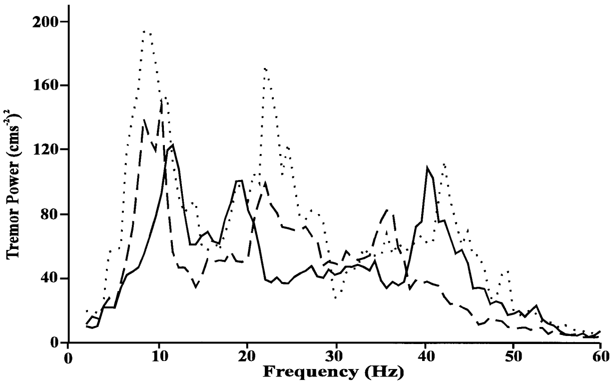


Fig. 3 Power spectra of tremor of three different subjects performing a 50% MVC of the first dorsal interosseous (1DI) against an elastic load showing three clear peak spectral frequency values in ranges around 10 Hz, 20 Hz and 40 Hz. Subject 1 (*solid line*) has median peak values at 11.5 Hz 19 Hz and 40.5 Hz; subject 2 (*dashed line*) has peaks at 9 Hz, 22 Hz and 36.5 Hz; subject 3 (*dotted line*) has peaks at 8.5 Hz, 22 Hz and 42.5 Hz. The exact median peak frequency values in these subjects thus indicate that no combination of frequency peaks always simply matches a harmonic series; in all three subjects the 10-Hz- and 20-Hz-range peaks are clearly not exact multiples, in subjects 1 and 3 the 10-Hz and 40-Hz peaks are not multiples, and in subjects 1 and 2 the 20-Hz and 40-Hz peaks are not multiples

are consistent with the peak intervals found in the tremor event histogram. The peaks were present to varying degrees in all the subjects studied. They were simultaneously present not only in spectra averaged over long recording sessions but also within individual 6-s recording periods. Over even shorter periods, the spectra were too noisy to distinguish peaks reliably. However, raw records did sometimes suggest that different oscillations could overlap in time. The peak frequencies were not exact multiples of one another in an individual subject (Fig. 3). Mean values of ten subjects and their standard errors are shown in Table 2. The 40-Hz peak was not always as sharply defined as the other two, sometimes being better described as a broad region of moderate power, but an obvious sharp peak in the 40-Hz range was obtained at least once in every subject and nearly always in some subjects. (At high levels of contraction there was sometimes also a suggestion of a rise in power at around 60–65 Hz, but this was a very inconsistent finding.) Factors that tended to blur the higher frequency peaks included fatigue, a poor compliance with keeping the finger stationary during the record and the presence of co-contraction of other muscles. These three factors were minimized in this study because subjects only needed to concentrate on making a steady contraction for 6 s at a time.

The frequency peaks of EMG activity were very similar to those found in the corresponding tremor power spectra (Fig. 4). On examination of the time domain records, it was seen that the peaks reflected the regular intervals between the polyphasic EMG bursts. A broad EMG spectral band at around 200 Hz was also seen; this probably reflected regularity of spike widths within a burst and the fact that full-wave rectification would result in a double peak from the positive and negative voltage deflections. The interval between these deflections was around 5 ms, resulting in an artefactual 200-Hz peak. Half-wave digital rectification performed on some records resulted in loss of this 200-Hz band but no other change in the data. The sharpness of the EMG spikes will also result in artefacts from the creation of odd-numbered, square-wave type harmonics.

Coherence analysis was performed between tremor traces and the corresponding EMG traces (Fig. 4C). There was a broad band of coherence between 5 and 80 Hz, but the coherence was particularly strong and much greater than the background level at the three frequency peaks common to the tremor and EMG signals. There was also sometimes a rise in coherence corresponding to the possible peak at 60–65 Hz. A constant phase relationship existed for the three main peaks (Fig. 4D). A peak was arbitrarily represented by four contiguous 1-Hz frequency bins (this value seemed optimally to reflect observed peak widths), and these bins were mapped onto the phase spectrum; it was seen that a constant slope fitted all three frequency peaks and cut through the origin (the phase change for a fixed time delay at d.c. should be zero). Phases at frequencies where there were no frequency peaks did not fit as well on this line. The fit was generally less good for the 10-Hz-range peak than for the two higher frequency peaks.

The constant negative slope of phase difference equated to a fixed time lag of tremor acceleration behind EMG of 6.5 ms. Phase plots of other data sets gave closely similar values. The raw records also show this very short lag on measuring from the middle of an EMG burst to the peak tremor acceleration (Fig. 2A). This value is not directly comparable with those generally cited for electromechanical delay. First, as discussed by Matthews (1994), measurements of phase are not equivalent

Table 2 Comparison of power spectra of ten subjects' tremor at three contraction strengths

	Frequency at 12.5% MVC (Hz) Mean/SE	Frequency at 25% MVC (Hz) Mean/SE	Frequency at 50% MVC (Hz) Mean/SE	Significance
Peak 1	9.4±0.43	9.4±0.35	9.9±0.36	$P = 0.13$
Peak 2	20.5±0.81	20.85±0.69	21.1±0.48	$P = 0.72$
Peak 3	40.1±0.51	40.3±0.37	39.8±0.34	$P = 0.5$

Significance refers to the *P*-value calculated from a repeated-measures ANOVA on the ten subjects' frequency values of one of the three peaks over the three different levels of contraction. In none of the three peak ranges is there any statistical evidence for a significant change in the frequency values on changing contraction strength

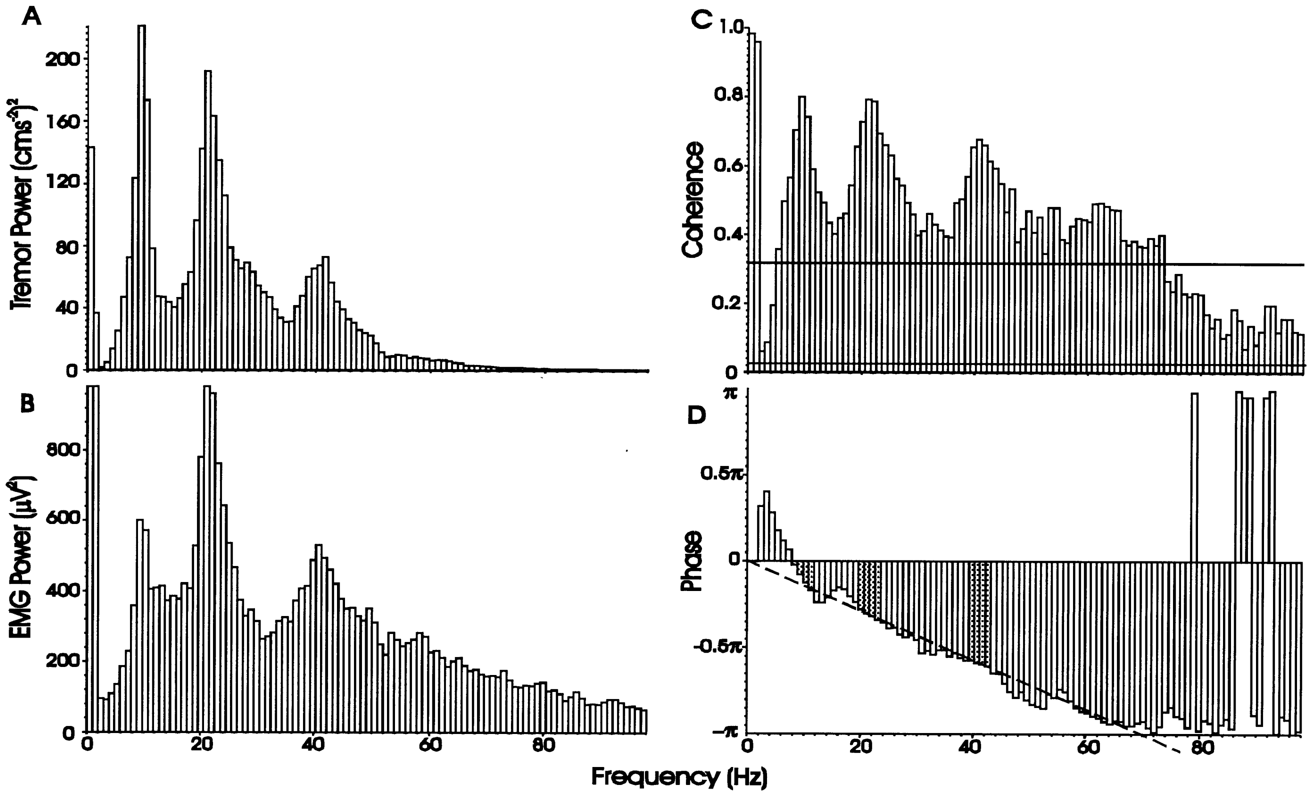


Fig. 4A–D Power spectral estimates and coherence analysis of a record made during an elastic 50% MVC. The data was accumulated from a fast fourier transform of 120 blocks of 2048 points, giving a bin width of approximately 1 Hz. The sampling frequency was 2008 Hz. Clear peaks are seen at 10 Hz, 22 Hz and 41 Hz in both the tremor power spectrum as measured by an accelerometer (**A**) and the simultaneously recorded rectified surface EMG power spectrum (**B**). The power scales on the *y*-axes are root-mean-square values, a measure of the variance of the acceleration and EMG signals. Coherence analysis between these records (**C**) reveals broad peaks of coherence in all three frequency bands. The *upper horizontal line* is the 95% confidence level at which the coherence at a certain frequency is significantly greater than the mean coherence over the whole spectrum. This gives a rough idea of peak versus background coherence levels. The *lower line* is, for comparison, the 95% confidence level for non-zero coherence (0.025 for 120 blocks). The phase plot (**D**), indicating the phase difference between the two signals at different frequencies, shows a constant linear relation at the coherent frequencies. The linear slope represents a constant time lag of the tremor acceleration of 6.5 ms behind the EMG for all three of the frequency peaks

to measurements of latencies from triggered time averages of repeated discrete twitches. Frequency analysis does not simply compare EMG onset with tremor onset but depends upon the overall duration and waveform of each EMG burst compared with each tremor fluctuation. Moreover, the averaging of data obtained in this way gives mean phase values, whereas averaging in the time domain will give the earliest latency values. The durations of polyphasic EMG bursts in this study were 10–20 ms, so an extra 5–10 ms should be added to the delay value if latencies are taken from EMG onset. Second, the measurements depend greatly on the mechanics of different experimental arrangements. The mechanical situation during a voluntary or electrically induced muscle twitch at rest is completely different from maintenance of modulation in an already active muscle. Measurements from rest may also severely overestimate the true latencies of initial muscle contraction (Corcos et al. 1992). Values for electromechanical conduction time extrapolated from single-unit twitch rise times (from which must be subtracted muscle action potential rise times) depend on whether they are obtained directly or by spike-triggered averaging and decrease significantly due to twitch fusion as the unit firing rates increase to the physiological range (Thomas et al. 1990). In any case, single-unit isometric twitches still represent a different mechanical situation from synchronized activity of highly fused units during an elastic contraction that favours high-frequency responses. The short-latency values in this study were therefore compared directly with electrically induced twitches of high frequency during elastic contractions. Peripheral electrical shocks to the ulnar nerve at 30 Hz resulted in extra peaks at this frequency in the EMG and tremor spectra, with the phase lag lying on the same line as the original three peaks. The short-latency values of this study may in fact be a more true reflection of the actual delay from electrical to mechanical activation of muscle fibres than previous studies measuring movement from rest or looking at averaged single-unit force profiles.

The most important point about the coherence analysis is that it shows that all the tremor frequency peaks were reflected in the EMG peaks with a fixed time relationship. It is considered unlikely that the multiple-tremor peaks simply represented harmonics created during

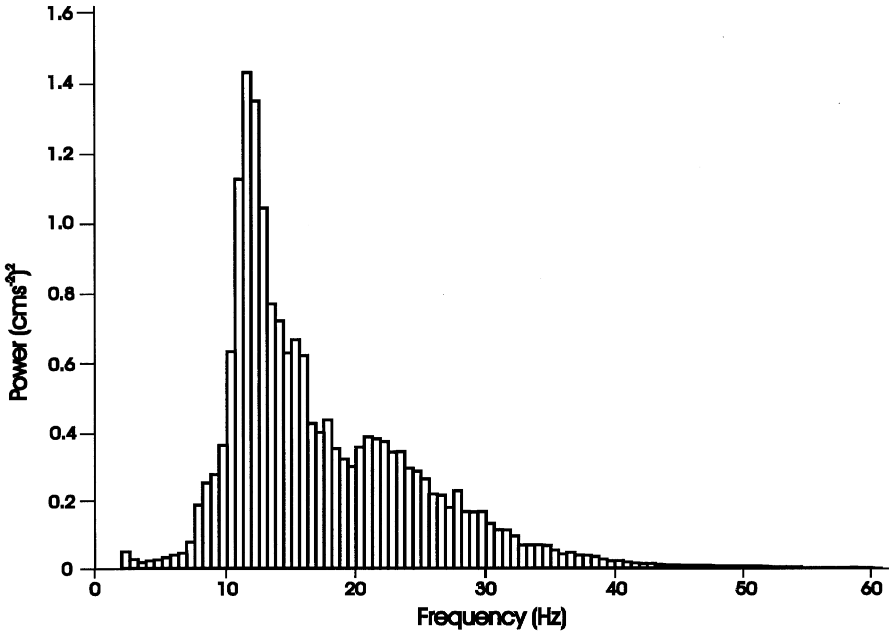


Fig. 5 Power spectrum of the finger held passively extended in the air with no added force to oppose. (The EMG of 1DI was silent in this condition.) A different pattern of peaks results, the most prominent one corresponding to the well-described 10-Hz-range peak found in the free outstretched limb

the recording and analysis of tremor acceleration. Since the EMG and tremor signals were so dissimilar in fine pattern, their harmonic series would be different in pattern and could not result in spectra that were so strongly coherent and phase-linked at all three frequencies. Other evidence against a harmonic source of frequency peaks is as follows. The raw records of integrated EMG and tremor clearly showed activity at all three frequencies, as reflected in the interval histogram of the tremor record. (The latter indicated that at least the 40-Hz peak was genuine. However, due to intermittent triggering, the interval histogram could generate wavelengths that were subharmonics of 40 Hz.) Finally, close inspection of the individual frequency spectrum records (Fig. 3) revealed that the three peaks were seldom at exact frequency multiples. Sometimes they varied from this pattern by more than the overall width of a peak, so that if a proposed harmonic peak were present it would be clearly distinguishable from the actual observed peak in that range. The peaks' shapes were also different from one another and did not become broader as frequency increased in the way that harmonics would be expected to behave.

The above results can be compared with previous studies looking at EMG and AMG rhythms during active contractions. For comparison with studies on tremor frequencies at rest, finger tremor was analysed while the subject held out his extended finger without the application of any abducting force. (This condition is generally referred to in this paper as being "at rest". Although the finger was elevated slightly, no 1DI EMG activity was recorded, in contrast to the condition where an active 1DI contraction was made against the elastic. Indeed, eliminating active elevation against gravity by supporting the outstretched finger using a flexible loop of thin wire resulted in no significant change in the power spectrum.) The power spectra at rest showed a complete absence of power at 40 Hz (not merely loss of a peak) and a more variable 20-Hz peak (Fig. 5). The 10-Hz peak was consistently present and was now the major frequency of oscillation, in accordance with accepted values for the tremor of free outstretched limbs (Marsden 1978). The power of this resting tremor peak was two orders of magnitude smaller than that of the 10-Hz-range peak of finger tremor when 1DI was actively contracting. In the resting situation, contamination from other sources such as the ballistocardiogram, other muscles and mechanical resonances may now contribute more significantly to the observed peak oscillation.

In the power spectra of resting records, there were sometimes also peaks at other frequencies, e.g. 15 Hz and 25 Hz, but these were different from those described above in that they were only present in certain subjects and in certain records. These peaks may have been mechanical contaminants or tremor transmitted from other parts of the body; they would have a greater relative power in the resting state because of the much smaller overall amplitude of finger tremor. Inconsistent peaks were also rarely observed in the power spectra of records during active contraction.

Effect of varying contraction strength

A systematic study was carried out to investigate the influence of different contraction strengths on the frequency peaks in the power spectrum; these strengths ranged from 12.5% to 50% MVC, the maximum isometric contraction that could be consistently maintained without fatigue. A typical result from one subject is shown in Fig. 6. The striking finding was that once a contraction occurred, even if modest, the frequencies of the peaks remained constant. (On weak contraction, the 40-Hz region did not always contain a clear frequency peak, but instead there was sometimes merely a broad band of

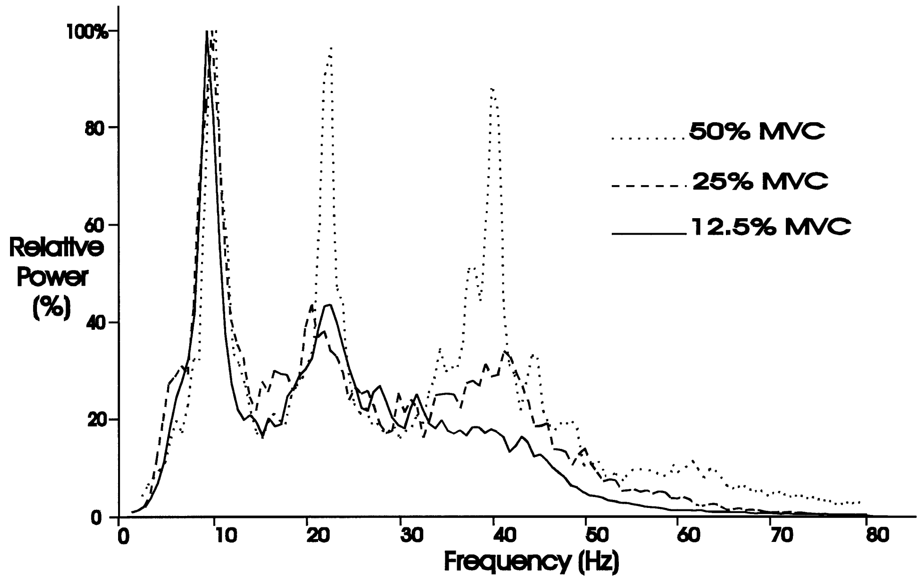


Fig. 6 Superimposed tremor power spectra of 1DI contractions of 12.5%, 25% and 50% MVC in one subject, showing that the frequencies of the peaks do not alter, but that the higher frequency peaks become relatively more prominent. This indicates that the peak frequencies are insensitive to changing mechanical parameters and that they are a constant feature at different levels of recruitment of motor units, where the *mean* rate of firing would be expected to increase. The *y*-axis scale is normalized so that the peak power of the 10-Hz-range peak in each trace is set at 100%. The overall power is much greater with stronger contraction; absolute 10-Hz-range peak power values for the 12.5%, 25% and 50% MVC strengths are 32 cm s^{-2}, 80 cm s^{-2} and 185 cm s^{-2}

moderate power in this range. This is in contrast to the tremor power spectrum on passive finger extension, where there was negligible power around 40 Hz; see Fig. 5. When a 40-Hz peak did occur on weak contraction, it similarly showed a lack of change in frequency on increasing contraction strength.)

To collate the results of all ten subjects, the frequency and power values of the peaks in each spectrum of each subject were quantified by arbitrarily setting a bandwidth of 6 bins (approximately 4 Hz) for a frequency peak. This value was chosen by observing the widths of frequency peaks in all the records and reaching a compromise between selecting for the total power in a peak and excluding neighbouring background power. To determine the power of a frequency peak, measurement was made of the power values of individual bins (of width 0.65 Hz) within an observed peak. The six contiguous frequency bins whose power when totalled gave the greatest value were determined. This totalled value represented the total power of a frequency peak and the central frequency of the six bins represented the frequency value of the peak. Where there was no clear peak in a power spectrum, a central peak frequency value was derived from the mean of the peaks in the other records of that subject and the quantified band was taken as the total power of frequency bins occurring at ±3 bins around this value. This was necessary for the 40-Hz range of three spectra at 12.5% MVC and one spectrum at 25% MVC.

It was found that the lack of change of peak frequency with contraction strength was reflected across all ten subjects as well as in individuals. Using repeated-measures analysis of variance for the ten subjects, there was no statistical support for a significant change in peak frequency values when occurring at three different contraction strengths (Table 2).

The total power of each frequency peak increased dramatically with increased contraction strength (i.e. increased elastic tension), indicating that the contraction became more tremulous. Although some subjects also had a *relative* shift in power towards the higher frequency peaks during stronger contractions (Fig. 6), this was not a consistent finding. These findings, along with the fact that units would not be able to maintain firing at 40 Hz, suggest that frequency peaks might not merely reflect the firing levels of individual units but may include an indirect modulation of the timing of firing of a population of units. In other words, especially at 40 Hz, a frequency peak does not necessarily mean that large numbers of individual units will be found to fire at that frequency. Instead, considering the population of units as a whole, the probabilities of firing are modulated so that more units will tend to fire on each pulse of an external rhythm than in the period between the pulses. According to the mechanism described, only multi-unit or surface recordings would reveal the pattern. This point was discussed by Elble and Randall (1976), who found that surface EMG was coherent with tremor at 8–12 Hz, even though needle recordings indicated that the motor units were firing at 10–22 Hz. The modulation of the probability of single-unit firing at a certain “tuned” frequency independent of mean unit firing rates has recently been directly demonstrated by Matthews (1994). In the present study, the observed changes in relative power of the frequency peaks might be due to variations in the strength of the different central oscillators rather than solely a manifestation of changing motor unit firing rates.

Mechanical oscillations

In order to distinguish peaks of neuromuscular activity from mechanical resonances, each trial in three subjects was repeated with the single difference that the finger/apparatus arrangement was plucked or tapped sharply by the experimenter in an attempt to bring out the mechanical resonance frequencies. This procedure resulted

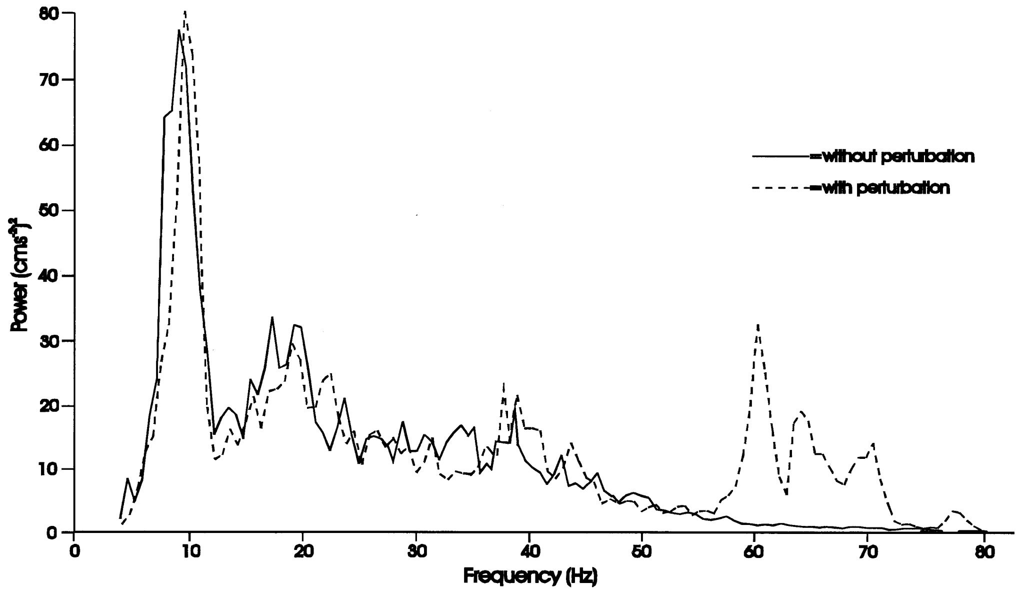


Fig. 7 Power spectrum of tremor during a 50% MVC in one subject with and without mechanical displacement in the form of irregular sharp taps on the finger and elastic. The three frequency peaks at 10 Hz, 20 Hz and 40 Hz are unaffected by these perturbations but the perturbations instead result in the addition of separate peaks at around 60–70 Hz. These new peaks are thought to be the natural mechanical resonance frequencies of the experimental arrangement and are therefore unrelated to the three main peaks described in this paper

in unchanged 10-Hz, 20-Hz and 40-Hz band peaks and the addition of an artefactual-looking peak at about 130 Hz and 65 Hz (Fig. 7). These latter peaks increased in frequency with increased tension on the elastic, while, as described before, the three physiological peaks remained unchanged. The mechanical peaks were also absent from the corresponding EMG spectra.

Muscle vibration recordings

An electronic heart-sounds stethoscope was applied over the 1DI muscle belly during elastic contractions in combination with simultaneous recording of tremor at the end of the finger. The power spectra of this muscle vibration (AMG) signal again showed three frequency peaks, which were coherent with the corresponding tremor peaks (Fig. 8). The presence of the AMG 10-Hz peak was unclear because of poor gain of the microphone at such low sound frequencies but the coherence spectrum revealed a clear peak at this frequency as well as in the 20-Hz and 40-Hz bands. Listening to this stethoscope subjectively resulted in the same sounds as those heard through other stethoscopes, suggesting that the frequency peaks recorded by these means might be responsible for the long-described findings of low-frequency rumblings on listening to contracting muscles. Comparable, but less clear, results were obtained using an accelerometer attached to the muscle belly in place of the sound monitor. The signal was of poorer quality than accelerometer recordings at the end of the finger, because the movement of the skin was much smaller than that of the finger. Contractions were now also performed against a fixed resistance, and AMG spectra consistent with the three frequency peaks were still obtained.

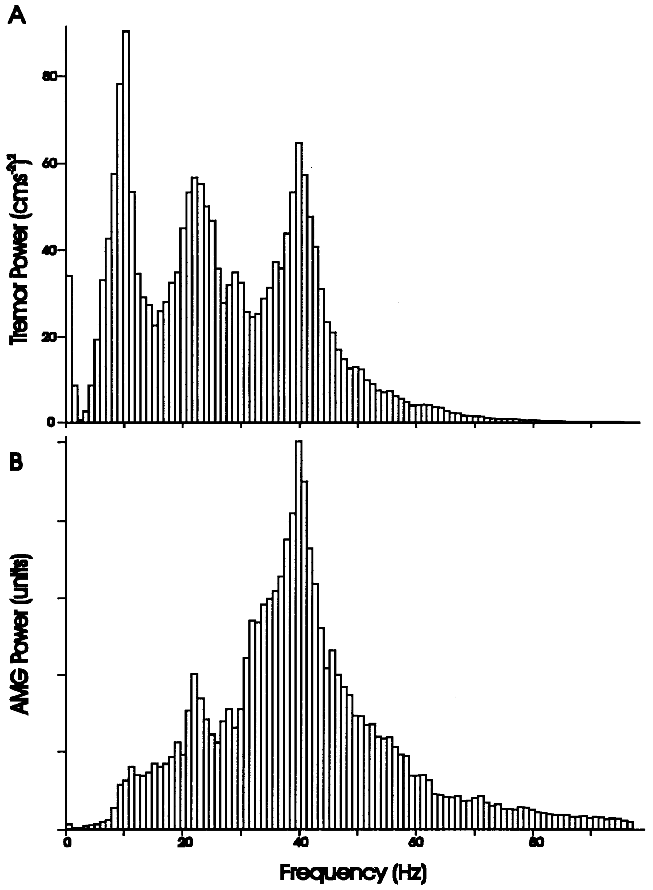
On coherence plots between tremor and muscle vibration (Figs. 8, 10), significant coherence was often also seen in a broad range at frequencies above 40 Hz. Since both power spectra revealed no clear peaks at these frequencies, and since the accelerometer and sounds monitor both essentially detect motion but merely in different locations, this coherence might simply be due to cross-talk between a variety of low-amplitude mechanical vibrations.

Effect of limb anaesthesia

The experiment was repeated in one subject under ischaemia-induced anaesthesia by using a sphygmomanometer cuff applied to the upper arm. The quality of the recordings was limited by the short time window available between total hand anaesthesia and total paralysis (Goodwin et al. 1972), by an inconsistent contraction due to 1DI weakness and by finger movement due to lack of proprioception. However, even under these highly abnormal conditions, clear peaks were preserved during severe anaesthesia (Fig. 9), when large afferents carrying proprioception (and important in stretch reflexes) were non-functional. This argued against peripheral feedback having the major role in the generation of the observed frequency peaks of muscle tremor. In another subject, contractions under lignocaine-induced anaesthesia of the ulnar nerve had a similar lack of effect on the frequency peaks.

Effect of loading of the finger

Loading of the finger with lead would be expected to lower peripheral feedback oscillation frequencies, by the increased inertia resulting in a greater delay from EMG bursts to resultant detection of motion by the afferent receptors. It would also be expected to lower mechanical resonance frequencies. In all three subjects tested with loading, moderate weights resulting in a significant in-



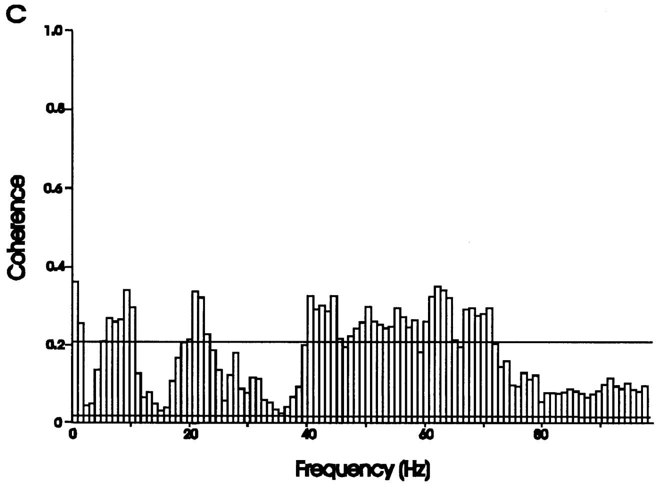
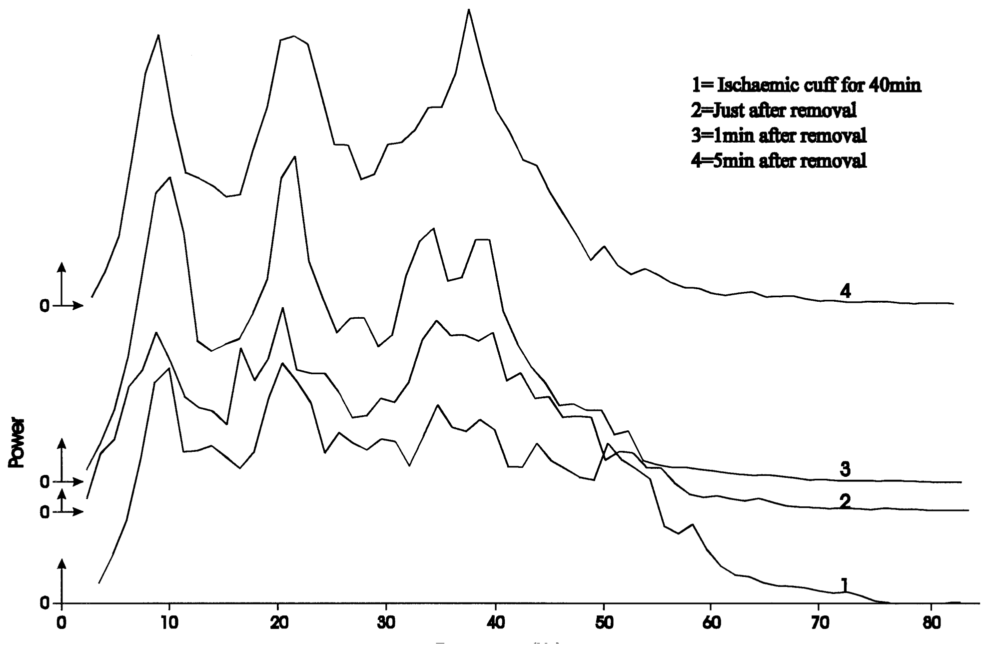


Fig. 8A–C Comparison of accelerometer tremor and simultaneously recorded 1DI acousto-myogram (AMG) during a 50% MVC. The latter was measured by a heart-sounds microphone placed directly over the muscle belly of 1DI. The power spectra of finger acceleration (**A**) and muscle acousto-myogram (**B**) show similar peaks of activity in the 20-Hz and 40-Hz bands; there is a suggestion of a small peak at 10 Hz in the AMG spectrum corresponding to a large peak here in the tremor spectrum. The coherence spectrum between acceleration and AMG (**C**) also shows a 10-Hz peak, indicating that the doubtful AMG peak represents the same oscillation as that picked up by the accelerometer. The heart-sounds microphone is not as sensitive at 10 Hz as at 40 Hz (the lower frequency limit of human hearing), which may explain the low power of the 10-Hz AMG peak

Fig. 9 Power spectra of tremor during anaesthesia of the limb, caused by 40 min of ischaemia. The *bottom record* was taken in a very short time window between anaesthesia and complete paralysis. The record directly above is just after removal of the cuff causing the ischaemia; the limb was still anaesthetised. The third and fourth records were begun 1 min and 5 min, respectively, after the cuff was released. The limb was still partially anaesthetised during the third recording but had subjectively recovered sensation by the last recording. The 10-Hz, 20-Hz and 40-Hz peaks are still present despite removal of peripheral feedback by anaesthesia and do not change in frequency. The overall tremor increased when the anaesthesia was more severe (N.B. traces *1* and *2* are plotted at approximately half the gain of *3* and *4*)



crease in the finger's moment of inertia did not change the frequency of the 10-Hz, 20-Hz or 40-Hz peaks (Fig. 10). Excessive weighting (70–140 g) resulted in the loss of the 40-Hz peak. Using the technique of applied mechanical perturbations, the increased inertia resulting from a 70-g weight was found to reduce the mechanical resonance frequency from 60 to 15 Hz. This dramatic change in the mechanical properties of the system will severly dampen high-frequency oscillations of any origin and so the loss of the 40-Hz peak is not surprising. The corresponding vibrations recorded directly from the muscle belly, and so less dependent on the mechanics of the

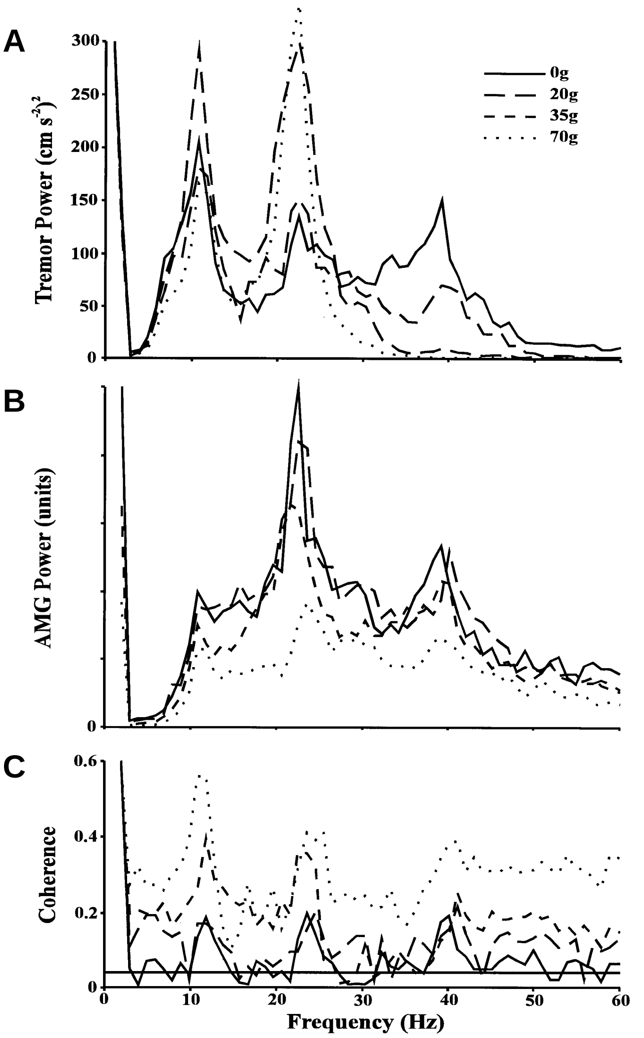


Fig. 10A–C Power spectra of tremor (**A**) and AMG (**B**) during contraction at 50% MVC with the addition of added loads in the form of lead strips wrapped around the index finger. The four spectra are each means of 80 blocks recorded in the same subject while unloaded and with loads ranging from 20 to 70 g. (The 70-g load was found in a separate experiment, not shown here, to reduce the measured mechanical resonant frequency to around 15 Hz.) The frequencies of the 10-Hz-, 20-Hz- and 40-Hz-range tremor and AMG peaks do not change significantly with loading. The 40-Hz-range peak is reduced dramatically in size with heavy loads but the preserved AMG and coherence (**C**) peaks indicate that modulations at this frequency are still present

finger, showed a 40-Hz-range AMG peak that is both preserved and unchanged in frequency on applying heavy loads (Fig. 10B). EMG spectra also sometimes but not always showed relative preservation of the 40-Hz peak with heavy loads. The coherence spectrum, which is independent of the absolute amplitude of oscillations, showed that the peak coherence at 40 Hz was maintained between AMG and tremor, indicating that the 40-Hz tremor peak was still present but too severely dampened to be detectable in the tremor power spectrum above background noise (Fig. 10C). The loading experiment thus indicates that elastic mechanical conditions did not generate but merely amplified a pre-existing, high-frequency oscillation. Since the mechanical conditions during heavily loaded elastic finger contractions are relatively closer to those while measuring force "tremor" during isometric (i.e. very high inertia) contraction (e.g. Homberg et al. 1986), this demonstration of the amplifying effect of elastic contraction may partly explain why only this and not previous studies have described the 40-Hz-range tremor correlate of Piper rhythm.

There was a tendency for the 20-Hz peak to decrease in frequency with excessive loads of 140 g; it must be noted that such a heavy loading completely changed the task so that as much effort was now directed to elevate the finger against gravity as to maintain horizontal position against the elastic. Different hand muscles have been shown to exhibit small but clear differences in frequency peak values in the 20-Hz range (McAuley and Brown 1995).

Discussion

It was shown that, during steady 1DI contraction against an elastic load, there exist not one but three peak oscillation frequencies at around 10 Hz, 20 Hz and 40 Hz. These findings are greatly strengthened by demonstrating that all three peaks are present in spectra derived from all three recording techniques, namely EMG, muscle vibration (AMG) and tremor (accelerometer). Previous investigations of rhythmic oscillations during contraction of hand and finger muscles have yielded conflicting results. They have generally concentrated on a single recording technique and described a single, important peak oscillation frequency. By employing elastic contractions, this study enables simultaneous recording of EMG, muscle vibration and tremor in the active state. Such contractions also tend to favour detection of higher frequency tremors and muscle vibrations in addition to that at the well-described 10-Hz frequency. The fact that there are indeed multiple peaks over a wider range may at least partially resolve the contradictory results in the literature. Perhaps previous studies on 1DI and similar muscles have used techniques favouring detection of frequencies over narrow and differing ranges, each revealing only one of the multiple peaks present.

The presence of multiple peaks raises the question that one or more are merely harmonics generated by the recording and analysis technique. Arguments against this are as follows: (1) the power, coherence and phase spectra all reveal the same pattern of three peaks using three completely different recording devices producing dissimilar signals that would result in different patterns of harmonic peaks; (2) regular intervals corresponding to the different peaks are seen in the raw tremor records and in the interval histogram, the latter indicating that at least the 40-Hz-band peak is a genuine tremor oscillation frequency; and (3) the peaks' shapes do not become broader and slurred at higher frequencies but instead have differently asymmetrical shapes in the same spectrum and the peaks' frequency values are not at exact multiples; the difference between an observed peak frequency and the expected harmonic is sometimes greater than the width of a whole peak.

Resting tremor

When recordings were made during gentle elevation of the finger with no active abduction, a 10-Hz-range peak frequency of tremor was found along with a smaller, more variable peak at 15–20 Hz. These results are consistent with those of previous studies looking at resting or postural tremor (Halliday and Redfearn 1956; Yap and Boshes 1967; Marsden et al. 1969a; Lakie et al. 1986) and are clearly different from those on active contraction against an elastic load. At rest, there was virtually no power at around 40 Hz, whereas even on modest 12.5% MVC contractions there was always considerable power at this frequency even in spectra where the 40-Hz peak was indistinct. The 10-Hz component was also much smaller in amplitude at rest than during activity, a finding previously noted by Marsden et al. (1969b) and by Vallbo and Wessberg (1993). Since no muscle activity takes place in the resting condition, the very small resting tremors are probably transmitted from other structures. These might include the ballistocardiogram and mechanical resonances or muscle vibrations from other body parts.

Muscle sounds

On listening through the electronic stethoscope used to record muscle vibration, we heard the same rumbling sounds as those described by others from contracting muscles (first reported by Grimaldi in 1665 and Wollaston in 1810; see Orizio 1993). Since exactly the same stethoscope set-up produced the three typical frequency peaks on spectral analysis of the signal, it may be that these peaks are responsible for the muscle sounds. The sounds heard appear subjectively to be at about 40 Hz, close to the lower limit of the frequency range of human hearing. The highest of the three frequency peaks is similarly at 40 Hz and, from the EMG records, is likely to be the same phenomenon as Piper rhythm. Muscle noises may therefore be the correlate of Piper rhythm.

Origin of the frequency peaks

The oscillations found in this study are due to *synchronized* firing of numbers of motor units, because their amplitudes are too great to be generated by single units [especially since a large amount of fusion is expected when single twitches, each of duration 50 ms (Thomas et al. 1990), are being generated every 25 ms for a 40-Hz oscillation] and because polyphasic activity at the peak frequencies, reminiscent of Piper rhythm, is seen in both surface and needle EMG records. Moreover, the considerable increase in power of the frequency peaks on increasing contraction strength without any shift in frequency strongly suggests that the peaks are due to contributions from increasing numbers of units synchronized by an external rhythmicity. These arguments together discount the possibility that any of the peaks are due solely to the firing characteristics of individual units, such as minimum, modal or maximum firing rates or different unit populations. A small degree of synchronization has been shown to occur purely by chance (Taylor 1962). However, the large increase in peak power with increased contraction indicates that the synchronization is robust and too powerful to be accounted for by such a mechanism. Nevertheless, a few relatively unfused units firing together by chance at 10 Hz might contribute significantly to the 10-Hz-frequency peak. At 20 Hz and 40 Hz, even if units could maintain firing at these frequencies, the forces generated by the very highly fused twitches would be negligible compared with the observed tremor fluctuations.

Synchronization at a certain driving frequency requires some external rhythmicity and is a different phenomenon from the short-term synchronization existing at all unit firing frequencies and believed to be due to common motoneurone inputs (Freund 1983). However, an external driving synchronization does not in itself imply that this rhythmicity originates from oscillations in the CNS. Mechanical resonances and peripheral feedback resonances could also generate such entrained activity (Stiles and Randall 1967; Joyce and Rack 1974; Marsden 1978; Matthews and Muir 1980; Freund 1983).

Mechanical resonances

The mechanical properties of the bone, muscles and soft tissues will have an influence on the frequencies of vibration of a body part, especially when recording at the end of the finger. The mechanical fundamental frequency of vibration, f_0, of any structure is related to its physical properties by the following equation (Walsh 1992):

$$f_0=1/(2\pi)\cdot(K/J)^{1/2}$$

where K is the stiffness or forces exerted on a structure and J is the moment of inertia. Even if the fundamental frequency does not result in an observed peak in an actively contracting system, it will still have a filtering influence so that another source of vibration of frequency widely different from f_0 will have to be of great power to exert a noticeable influence. An experiment that involved loading the finger or choosing a larger body part to investigate would thus bias strongly against the detection of higher peak frequencies, whereas using an elastic force, as in this study, would bias towards higher frequencies. When the finger is now heavily loaded, the relative preservation of the 40-Hz AMG power spectral peak and preserved coherence with tremor despite disappearance of the tremor peak confirm that the mechanical properties merely amplify rather than generate this peak oscillation. An important assumption to be made in considering an elastic force is that it should remain constant for different phases of the vibration. Since the length and properties of the elastic chosen in this experiment were such that the amplitude of the tremor was negligible compared with the distance of stretch on the elastic, it was felt that this assumption was valid.

Mechanical resonances of the unloaded finger are generally quoted to be 25–27 Hz (Stiles and Randall 1967), but these values are not relevant when an elastic force is applied. Therefore the apparatus/finger arrangement was sharply perturbed in some trials, so that the frequencies of the waning oscillations resulting from these taps, which reflect the fundamental frequency, would be superimposed on the power spectrum. These new peaks were at 130 Hz and 65 Hz and, unlike the "physiological" peaks, their frequencies increased with greater contraction induced by greater tension on the elastic.

The fact that the EMG records show peaks that are coherent in frequency and phase with the tremor peaks is suggestive of a neuromuscular origin. However, as Adrian (1925) pointed out, mechanical resonances could entrain afferent responses to modulate at the same frequency, which, in turn, might entrain the EMG via the reflex pathway. Anaesthetising the limb by ischaemia would block this mechanism, but the peaks were found to be preserved. Moreover, loading the limb with moderate weights sufficient to cause a profound drop in mechanical resonant frequencies and increasing the elastic force, which would increase resonant frequencies, had little effect on the main peak frequencies. Hagbarth et al. (1983) recorded single nerve afferents during runs of Piper rhythm and found no modulation of these afferent signals at this frequency, similarly suggesting that Piper rhythm is not generated by peripheral feedback transmitting mechanical resonances or setting up a feedback loop resonance. In summary, there is no evidence to support a mechanical origin of any of the three main peaks at 10 Hz, 20 Hz and 40 Hz described in this study.

Peripheral feedback

The tonic stretch reflex can be regarded as a negative feedback loop. If the loop is underdamped, the oscillations will tend to occur with a period of double the loop time. For example, the loop time for the spinal segmental stretch reflex in the finger, including the time from EMG to development of a movement detectable by the afferent receptors, is about 50 ms (Marsden 1978) and would therefore tend to create oscillation at 10 Hz. As well as this peak, a series of odd harmonics could result in reflex loop modulations at 10 Hz, 30 Hz, 50 Hz, etc. of a "white-noise"-type descending input (i.e. resonance at loop times equalling 0.5 cycles (fundamental), 1.5 cycles, 2.5 cycles). Oscillation due to the long-latency stretch reflex (which probably dominates the spinal reflex in the finger) would be at 7 Hz (Marsden 1978). Although neither short- nor long-latency reflex loops can easily account for the observed peaks, if they co-existed they might interact together or with other modulations to generate other patterns of peak oscillation frequencies (Matthews 1993). Nevertheless, in this study there was preservation of all the frequency peaks and their frequency values both under anaesthesia, when there is severely abnormal peripheral feedback, and with the addition of extra loads, where increased feedback delays would be expected.

Central origin

It therefore seems most likely that the observed peak frequencies of oscillation at 10 Hz, 20 Hz and 40 Hz are indeed manifestations of central oscillators. Many previous studies, including those by Vallbo and Wessberg (1993), Farmer et al. (1993a,b), Hagbarth et al. (1983), Keidel and Keidel (1990), Murthy and Fetz (1992) and Conway et al. (1995), also favour such an origin for peripheral rhythms; the latter three reports have directly demonstrated a correlation between central and peripheral oscillations. The importance of high-level processing in the production of tremor frequency peaks is clearly illustrated by studies showing that they can be influenced by visual feedback (Sutton and Sykes 1967), implying a central modulation of peripheral tremor. Closing the eyes resulted in the loss of a 10-Hz hand tremor peak, and the frequency of this visually dependent peak could be shifted by introducing artificial feedback delays. The latter manoeuvre revealed that there was also an underlying non-visual peak at the original frequency (Merton et al. 1967; Dymott and Merton 1968). However, there still remains considerable evidence from other literature to suggest a peripheral origin for 10-Hz-range oscillations (Table 1). It is at this peak frequency that random synchronization of single units firing at their minimum rate and peripheral feedback loop resonances are most likely to be manifest. Despite the great increase in power with contraction force and the lack of effect of loading or anaesthesia, peripheral factors might still *contribute* to, although not wholly account for, the 10-Hz-peak oscillation observed in this study. A multifactorial origin of the 10-Hz peak might explain the suggestion of a rise in mean 10-Hz-range frequency with increased tension and why the 10-Hz peak matches less well with the linear phase relationship between tremor and EMG than do the 20-Hz and 40-Hz peaks.

A number of different central oscillation mechanisms could generate the multiple, peripherally manifest frequency peaks found in this study:

1. The 10-Hz, 20-Hz and 40-Hz peaks could each arise from a separate central oscillator. The three oscillators running at the three different frequencies could exist in any CNS structure from the spinal cord upwards. Such frequencies are indeed strongly represented in the electroencephalogram (EEG) and magnetoencephalogram (MEG) as the α, β and γ spectral activity bands.

2. One of the peak frequencies could represent a fundamental central oscillation, while the other two modulations are merely harmonics of this fundamental derived at a later stage of processing of motor commands within the CNS. For example, the 10-Hz and 20-Hz oscillations might be subharmonics of a 40-Hz fundamental. However, if this is the case, the behaviour of the oscillator must be highly non-linear, since the observed 10-Hz and 20-Hz peripheral rhythms are clearly not at exact subharmonic frequencies and the expected 13-Hz peak (every third "tick" of a 40-Hz "clock") is not seen.
3. Finally, a single CNS oscillator of much higher frequency, such as that demonstrated at around 200 Hz on direct central recording by Buzsaki et al. (1992) and by Brown (1995a,b), might generate certain subharmonic frequencies that become manifest in the periphery. If oscillators had some role in the timing of output signals and correlating the arrival of input signals, a fast fundamental frequency of 200 Hz would be appropriate for the accuracy requirements of the nervous system. A high-frequency progenitor could explain the independent phases of 10- to 40-Hz oscillations sometimes recorded in the brain (Salmelin and Hari 1994) and in the periphery (Marsden et al. 1969b; McAuley and Brown 1995). For example, 40-Hz subharmonics derived separately from a single fundamental may behave independently, whereas a widespread 40-Hz oscillation should exhibit a constant phase relationship between recordings from different CNS or peripheral structures. The peaks at non-exact frequency multiples in this study also suggest that a single linear oscillator associated with all movements would be of high frequency; only in this case would many different potential subharmonics exist at frequencies that are not simply arithmetically related. However, a mechanism would now have to exist to explain why only a few of the many mathematically possible subharmonics in the 10- to 40-Hz frequency range actually become manifest.

It has previously been proposed that central oscillations in the 10- to 40-Hz range may have a role in "feature linking" during sensory information processing (Eckhorn et al. 1988; Gray et al. 1989) and during cerebellar processing of motor commands (Welsh et al. 1995). The multiple coexisting central oscillations of this study, whether originating separately or as certain selected harmonics of a high frequency fundamental, suggest the possibility that precise frequencies and combinations of frequencies of modulation may also aid in coding of motor commands. Further study of the peripheral manifestation of such oscillations might prove a useful way of investigating this possible role in human motor control.

In conclusion, this study presents data showing the presence of multiple synchronized rhythms of motor unit activity and suggests that they are a manifestation of rhythms occurring in the CNS. It is postulated that these rhythms may reflect the presence of central "timing" mechanisms that have a role in coding of movement commands.

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