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OSCILLATION OF THE HUMAN ANKLE JOINT IN RESPONSE TO APPLIED SINUSOIDAL TORQUE ON THE FOOT

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SUMMARY

1. Low-frequency (3–30 Hz) oscillatory rotation of the ankle joint in plantarflexion–dorsiflexion was generated with a torque motor. Torque, rotation about the ankle and electromyograms (e.m.g.s) for the gastrocnemius–soleus and the anterior tibial muscles were recorded.

2. Fourier coefficients at each drive frequency were used to calculate the effective compliance (ratio of rotation and torque). The compliance has a sharp resonance when tonic, voluntary muscle activity is present.

3. The resonant frequency of compliance is between 3 and 8 Hz. The location of the resonant frequency and the magnitude of the compliance at resonance depend upon both the degree of tonic muscle activity and the amplitude of the driving torque. The resonant frequency increases with increasing tonic activity.

4. With tonic muscle activity, the compliance in the frequency range below resonance increases with increasing amplitudes of driving torque.

5. The e.m.g., when evoked by the rhythmic stretch, lags the start of stretching by between 50 and 70 msec.

6. When tonic muscle activity is present, the resonant frequency of the stretch reflex is between 5 and 6·5 Hz.

7. Following the start of driven oscillation at frequencies near resonance, slowly increasing amplitudes of angular rotation (to a limit) are observed.

8. Distortion (from the sinusoidal wave shape) of angular rotation is frequently observed with drive frequencies between 8 and 12 Hz during which there sometimes occur spontaneous recurrences of oscillation at the drive frequency. For the angular rotation, a significant portion of the power may be in subharmonic frequency components of the drive frequency when that frequency is between 8 and 12 Hz.

9. Self-sustaining oscillation (clonus) near the resonant frequency of the

compliance is sometimes observed after the modulation signal to the motor is turned off. This is most often seen when the gastrocnemius–soleus muscles are fatigued. Clonus may be evoked by driven oscillation at any frequency.

10. The hypothesis that physiological tremor, which occurs between 8 and 12 Hz, is a consequence of stretch reflex servo properties seems to be at odds with the observations of resonance in the compliance and of self-generated clonus both occurring in the 5–8 Hz region.

INTRODUCTION

The dynamic properties of muscle contraction and its neurological control mechanisms have been extensively studied by the application of sinusoidal length changes. Sinusoidal oscillation is easy to generate and the methods of analysis are well understood. In linear systems, the mathematical analysis based on the transfer function and the phase relationship between the input and output variables provides a complete description of system behaviour. Sinusoidal input analyses have been performed by many investigators on various components of the system, particularly on the stretch receptors (muscle spindles) as well as on the total neurological control mechanisms operating at a joint.

The response of stretch receptors to sinusoidal stretching or to vibration has been investigated by Lippold, Redfearn & Vuco (1958), Bianconi & Van der Meulen (1963), Stuart, Ott, Ishikawa & Eldred (1965), Brown, Engberg & Matthews (1967), Matthews & Stein (1969), Rosenthal, McKean, Roberts & Terzuolo (1970), Poppele & Bowman (1970), and Westbury (1971). (See Matthews (1972) for a comprehensive review.) In most animal studies of the complete operating mechanism, the end of the muscle (or the joint) is subjected to displacement by a device which is significantly more powerful than the opposing muscle. The neuromuscular response, obtained as a variation in the tension or torque, exerted against the stretching of single muscle or muscle groups has been investigated in cats by Partridge & Glaser (1960), Roberts (1963), Rack (1966), Jansen & Rack (1966) and Poppele & Terzuolo (1968).

The animal studies mentioned above have the advantage of permitting subsystem analysis and recording at various points within the system (such as recording from the alpha motoneurones), but these studies do not provide information concerning functional physiological mechanisms, nor are they in humans. Joyce, Rack & Ross (1974) studied the forced oscillation of the human elbow joint. Many of their results are confirmed by those to be reported here. Berthoz & Metral (1970) and Neilson (1972) used similar techniques, applying a sinusoidally varying force while measuring elbow position. Walsh (1973, 1975*a*) applied sinusoidally varying forces to the wrist and observed a resonance and jump phenomenon. Burke, Andrews & Gillies (1971) studied the sinusoidal stretching response in spastic human subjects at frequencies less than 2 Hz with stretch applied manually by the experimenter. Duggan & McLellan (1973) used a technique similar to Walsh to measure the muscle tone at the elbow joint.

In this paper we will consider the effects of low frequency (3–30 Hz) forced sinusoidal oscillation of the ankle joint in normal human subjects. The resistance of the foot to movement is due to several factors. The limb presents an inertial load to an applied torque, the muscles offer visco-elastic resistance to lengthening and in addition, movement will be affected by active muscle contraction, both reflex and voluntary. In practice it is difficult to separate and measure these three resisting forces. The inertia of the limb probably remains constant but the resistance of muscles to lengthening and the intensity of stretch evoked reflexes are dependent on a number of interacting physiological variables, among them being the degree of muscle contraction.

The present investigation differs from Walsh (1971, 1973) and Joyce *et al.* (1974) works in two ways: first, in their work the frequency range was swept in a few seconds and single frequencies were not studied; second, the fly-wheel mechanism used by Joyce *et al.* (1974) applied a sinusoidal displacement rather than sinusoidal torque. In a non-linear system, displacement and torque inputs are not equivalent. They show different aspects of this complex system (Roberts, 1963; see also Berthoz, Roberts & Rosenthal, 1971).

Driven oscillation of the ankle joint in the frequency range of 8–12 Hz produced many striking patterns of rotation. Driven oscillation near the resonant frequency produced temporary fatigue in the muscles and an apparent instability of the ankle motor system manifested by clonus in normal subjects (Gottlieb & Agarwal, 1977). This 'physiological clonus' appears similar to pathological clonus (Grinker & Sahs, 1966). Joyce *et al.* (1974) predicted a possible instability in the motor system and the development of clonic oscillations. Walsh (1971) observed beating phenomena in the ankle joint which he related to ankle clonus. Some results of these experiments have already been briefly reported (Agarwal & Gottlieb, 1975*a*, *b*).

METHODS

Experiments were done on normal, adult, male human subjects. A subject sat in a chair with his right foot strapped to a footplate which could rotate about a horizontal, dorsal–plantar axis through the medial maleolus. A diagram of the equipment used is shown in Fig. 1.

The plate is rotated by a d.c. torque motor (Inertial Motors Corp. no. 06–024) via a gearbelt and pulley system for torque amplification. Constant tension springs (not shown in the figure) are also used to balance the plantar gravitational torque. With the subject completely relaxed, the resulting joint position (approximately

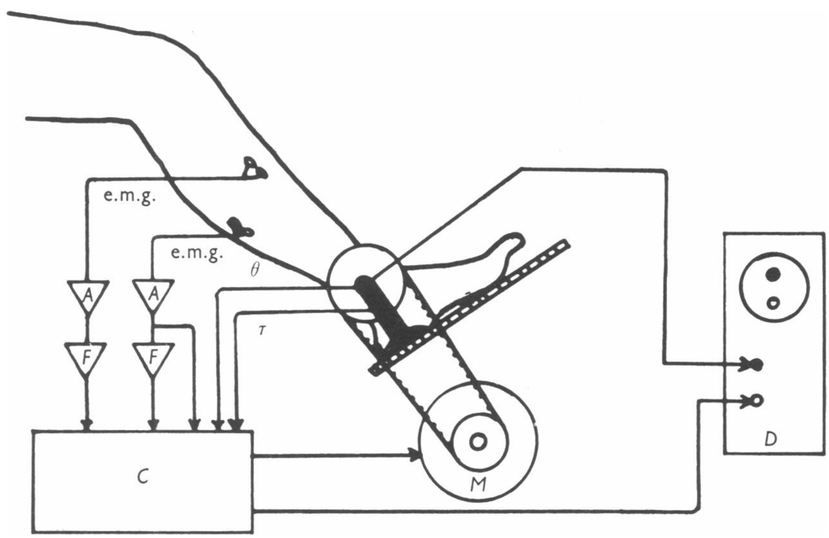

Fig. 1. A diagram of the apparatus used for the forced oscillation of the ankle joint. The components are: d.c. Torque Motor (M) driven by a Bulova power amplifier. Electromyograms (e.m.g.s) are measured using disk-surface electrodes placed over the bellies of the soleus and anterior tibial muscles, e.m.g. amplifiers (A) are Tektronix 2A61 (bandwidth 60–600 Hz), filters (F) are third order averaging (10 msec averaging time), display oscilloscope (D) is a dual-beam Tektronix 502, digital computer (C) is a General Automation SPC-16/65. Motor torque, τ; foot angle, θ.

90° between the foot and the tibia) defines the zero reference angle position. A dual-beam oscilloscope provides the subject with visual feed-back of his foot angle on one channel and the reference position on the other.

Sinusoidal signals were superimposed on a mean motor torque level. Frequencies from 3 to 30 Hz were used. The subject was instructed to try to maintain a constant mean force against the bias torque of the motor so that the oscillation was nearly symmetrical with respect to the reference angle. This was accomplished with little difficulty by all subjects.

The motor input voltage was $B+A \sin(2\pi ft)$ volts, where B is the bias voltage, A is the amplitude of modulating sinusoid and f is the drive frequency. For each sequence, B and A were constant and the response was observed at up to twenty-four frequencies. Frequencies from the high and low portion of the spectrum were applied alternately. These frequencies were from the set: 3, 3·5, 4, 4·5, 5, 5·5, 6, 6·25, 6·5, 6·75, 7, 7·5, 8, 8·5, 9, 9·5, 10, 10·87, 11·9, 12, 13·8, 15, 15·6, 17·8, 20, 25, 30, 31·25 Hz.

The torque was measured by a strain-gauge bridge on the side arms of the footplate. Angular rotation was measured by a continuous potentiometer. Electromyograms (e.m.g.s) were recorded from disk surface electrodes placed over the bellies of the soleus (*GS*) and anterior tibial (*AT*) muscles. These were amplified, full-wave rectified and filtered (10 msec averaging time) before recording. The filter characteristics are given in Gottlieb & Agarwal (1970). Details concerning torque measurement are reported in Gottlieb, Agarwal & Stark (1970).

The measured torque from the strain-gauge bridge is given by the following equation:

$$\tau_{\text{measured}} = -\tau_{\text{motor}} = \tau_{\text{contractile}} + \tau_{\text{mechanical}}.$$

The mechanical torque term is given by

$$\tau_{\text{mechanical}} = J\frac{d^2\theta}{dt^2} + D\frac{d\theta}{dt} + K\theta,$$

where θ is the angle of rotation, K is the angular elastic stiffness of the joint, D is the angular viscosity coefficient, and J is the moment of inertia of the foot and the plate with respect to the axis of rotation through the medial maleolus. The moment of inertia of the foot is estimated to be 107 kg.cm^2 for an average adult, male subject (Hogins, 1969).

A computer (General Automation SPC-16/65) generated the motor-drive voltage at a conversion rate of 1000/sec and digitized data on four channels. The applied torque, the resulting angular rotation and the two e.m.g.s were stored on digital magnetic tape. The angle and the torque signals were sampled at a rate of 250/sec and the filtered e.m.g.s at a rate of 500/sec. The data were continuously recorded for 16 sec, the first 11 sec of which the motor was driven at a particular frequency and for 5 sec after the modulating signal was stopped. The motor bias voltage was constantly applied throughout the 16 sec.

In some experiments, oscillation near 6 Hz was applied continuously for nearly 100 sec which produced muscle fatigue. Self-generated oscillations were observed after the modulating signal to the motor was stopped.

In most of the experiments reported here the applied voltage to the motor was a sinusoid of constant amplitude. The actual motor torque sometimes varied in amplitude and wave form due to the back electromotive force (e.m.f.) of the motor.

All recent experiments have been done using a torque feed-back servomechanism which makes the torque input dependent solely upon the driving input signal and independent of the foot's rotational velocity. All phenomena described here have been reproduced on both systems. Experiments using this servo appear in Fig. 10.

Data analysis. Fourier coefficients at the drive frequency were obtained from the torque and the angular rotation using 10·24 sec of the oscillation data. The analysis was done for twenty consecutive intervals of 0·512 sec duration each. The sine and cosine coefficients were used to compute amplitudes and phase angles for each of the twenty records and resulting twenty values were averaged. The effective compliance of the muscle system is defined by taking the ratio of the Fourier coefficients of the angular rotation and the measured torque at the drive frequency. For simplicity, the values of compliance are computed as if they were produced by a single muscle. It should be understood that this ratio is not the true muscle compliance, but is a measure of effective mechanical compliance of the entire joint and the foot-plate (Lang, 1975).

Let θ denote the amplitude of the angular rotation in radians, τ the applied sinusoidal torque in Newton metres, and R the radius of action of the muscle in metres. For plantar as well as for dorsal movements, the radius of action R is roughly 5 cm in an adult male of average size, although it varies slightly with the angle of the foot (Hogins, 1969). The effective change in the muscle length $\triangle L$ is then equal to θR and the effective change in the applied force at the muscle $\triangle F$ is equal to τ/R.

Effective equivalent compliance for the muscle

$$= \frac{\triangle L}{\triangle F}$$

$$= \theta R/(\tau/R)$$

$$= \frac{\theta R^2}{\tau}\ \text{m/Newton}.$$

For the compliance curves shown in Figs. 8–10, the value of R is taken as 5 cm for all subjects. The phase angle of the angular rotation is measured with respect to the motor torque and lags it at all frequencies tested.

Subject sample. The data reported here are from three of the ten subjects tested, two of them being the authors. Only two subjects were tested on both the right and the left legs (Fig. 10). The tense leg experiment in Fig. 10 was duplicated on three subjects.

Data presented in Figs. 3, 4, 6–8 are from the same experiment. Similar observations have been made in more than ten other subjects. The observation of Fig. 5 was seen only in this subject (a similar response was also obtained at 25 Hz drive) and has not been reproduced in any other subject.

RESULTS

At frequencies below 3 Hz the subject generally reacts to each individual cycle of stretch. The resulting rotation is a flattened out sine wave and extremely variable from cycle to cycle. For this reason the data presented cover the range from 3 to 31·25 Hz. At most frequencies, when the ankle joint is driven by a sinusoidal torque, the foot resists movement with a torque that also varies nearly sinusoidally and the resulting movement is nearly sinusoidal.

When the frequency is in the range from 3 to 6 Hz, subjects feel that they have very little control over individual cycles of oscillation. In most cases where the gastrocnemius–soleus muscle is tonically active against a bias torque, when the modulation is turned on we observe slowly increasing amplitudes of oscillation as shown in Fig. 2. As the oscillation amplitude increases, the applied torque amplitude decreases (primarily due to the back e.m.f. in the motor). The ratio of angle to torque amplitudes for successive cycles increases, approaching a plateau which indicates a dynamic change in the joint compliance. The e.m.g. amplitude of the gastrocnemius–soleus muscle increases as the amplitude of oscillation increases. The e.m.g. activity in the anterior tibial muscle also grows but is of considerably lower amplitude than the activity in the gastrocnemius–soleus muscle. The gastrocnemius–soleus e.m.g. bursts occur at about 50–55 msec from the start of the stretches in the dorsal direction. In this and all subsequent figures, upward movement is in the dorsal direction.

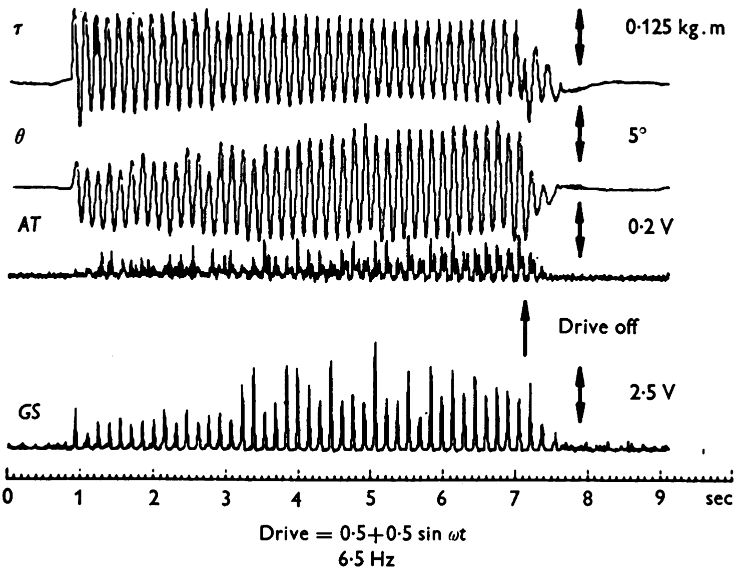

Fig. 2. Slowly increasing amplitude of oscillation near the resonant frequency of 6·5 Hz. The gastrocnemius–soleus muscles were tonically active, producing an average torque of about 0·2 kg.m. In this and the following figures, the four traces are the motor torque (τ), foot angle (θ), anterior tibial muscle e.m.g. (*AT*) and soleus muscle e.m.g. (*GS*). The e.m.g. scales are in volts after amplification, rectification and filtering of the surface e.m.g. (Subject G.L.G.).

In the frequency range of 8–12 Hz we have frequently observed striking non-sinusoidal wave forms in the oscillation of the ankle. Fig. 3 shows oscillation at a drive frequency of 12 Hz. The left portion of this figure shows steady-state driven oscillation after the drive had been on for 10 sec. Alternate stretch cycles are small and are not effective in producing any reflex e.m.g. activity. The e.m.g. activity is evoked only by the large stretch cycles. At about the 11 sec mark, modulation is turned off but the motor bias continues. The oscillations between the 11 and 12 sec marks are produced by the stretch reflex arc. The motor modulation is turned on again near the 13 sec mark. For the first few cycles, rotation of the foot occurs at the motor drive frequency and there is e.m.g. activity in gastrocnemius–soleus corresponding to each stretch phase. Non-sinusoidal rotational behaviour becomes progressively evident as alternate motor torque cycles become less effective in producing rotation. The small stretches of these alternate cycles do not produce any measurable e.m.g. response and the e.m.g. bursts are at half the driving frequency.

Fig. 4 shows the response of the subject at 10 Hz during the same experiment. In addition to the non-sinusoidal nature of the oscillation,

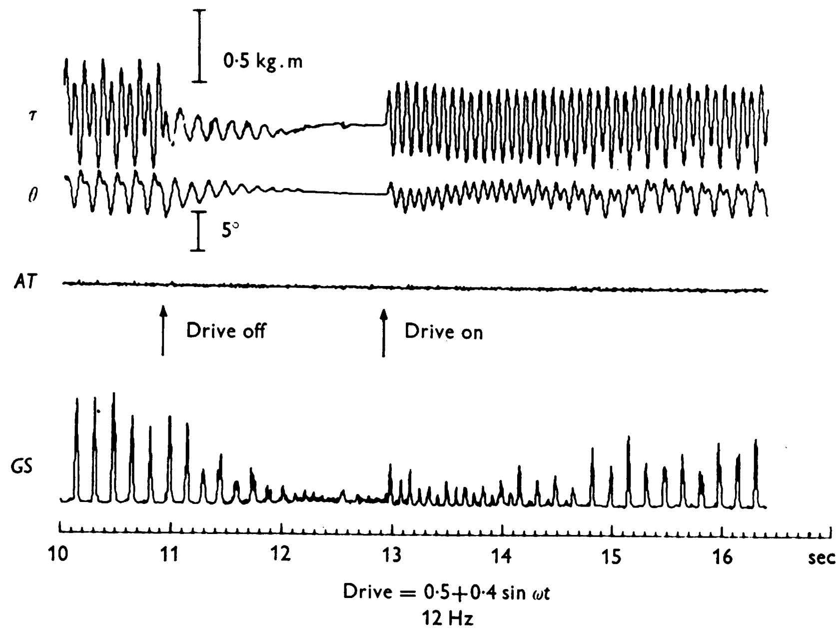

Fig. 3. The forced oscillation at a drive frequency of 12 Hz. The arrow indicates when the modulation signal of the motor was turned off after nearly 11 sec of continuous oscillation. The self-sustained oscillation of the foot continued for nearly a second at about 6·5 Hz. The modulating signal was turned on again near the 13 sec point. For the first 1 sec, the angular rotation was at 12 Hz with corresponding soleus e.m.g. activity and then gradually the non-sinusoidal nature of the oscillation became dominant and stable. This was also true at 11 Hz drive. In this and the next figure, the gastrocnemius–soleus muscles were tonically active producing an average torque of about 0·2 kg.m. (Subject G.C.A.).

spontaneous recurrences of oscillation at the driving frequency (indicated by lines below the angle of rotation curve) and a corresponding 10 Hz bursting in the soleus e.m.g. are observed for several cycles between intervals of non-sinusoidal oscillation.

Figs. 3 and 4 also show autonomous oscillation of the foot occurring after the modulating signal to the torque motor stops. In Fig. 4 this oscillation (in the 12–15 sec interval) is at 6·35 Hz as determined by Fourier transform analysis. Such self-sustained oscillations are always near the resonant frequency (see below) and not at the drive frequency.

These oscillations are *not* voluntary in nature and are *not* the transient response of an underdamped mechanical system since this oscillation has been observed to last from a few cycles to as long as 60 sec. Sustained motor-driven oscillation of the foot at frequencies near resonance is very

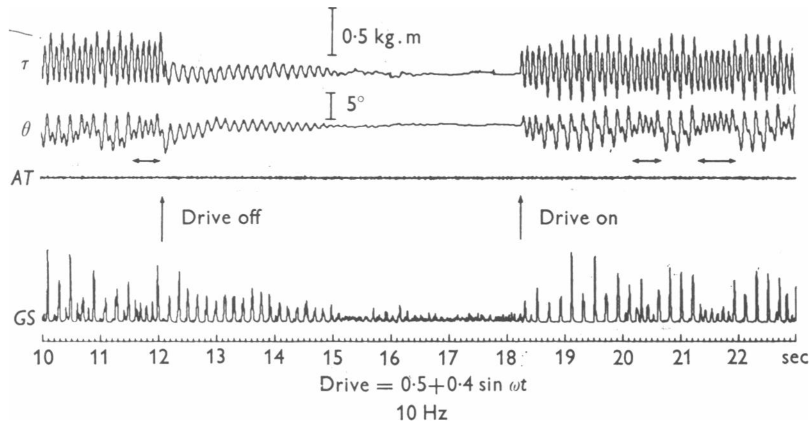

Fig. 4. The forced oscillation at a drive frequency of 10 Hz. The arrow indicates the time when the modulation signal of the motor was turned off. The self-sustaining oscillation of the foot continued for several seconds near 6·35 Hz as measured from the Fourier transform analysis. As the modulation signal was turned on again, the non-sinusoidal wave form rapidly developed. Recurrences of 10 Hz oscillation in between the non-sinusoidal response are indicated by line segments underneath the angular rotation curve. (Subject G.C.A.)

fatiguing to the soleus muscle. Such fatigue appears to be a favourable condition for the appearance of self-sustained oscillation in normal subjects.

Fig. 5 shows responses from another subject with the motor drive at 31·25 Hz. Only a small rotation of the foot is produced at 31·25 Hz drive because the foot and the footplate present a large inertial load to the motor. Clonic oscillation at 6·25 Hz begins immediately and dies out in about 1 sec after the motor drive is turned off. The left portion of the figure shows the turning on of the motor modulation and the initial stretch reflex in the gastrocnemius–soleus muscle.

Responses such as those in Figs. 3 and 4 are frequently observed when the motor bias torque tends to dorsiflex the foot and the soleus is in tonic opposition. Non-sinusoidal and self-sustained oscillation are only occasionally observed in experiments on normal subjects with zero bias or plantar bias (the anterior tibial muscle tonically active against the motor bias torque).

Due to the nature of the non-sinusoidal responses observed in Figs. 3

and 4, a two-cycle averaged response was calculated. The averaging was initiated by searching for the most plantar position of the foot from the start of the angular recording and then taking successive intervals equal to twice the modulation period (rounded to be a multiple of 4 msec

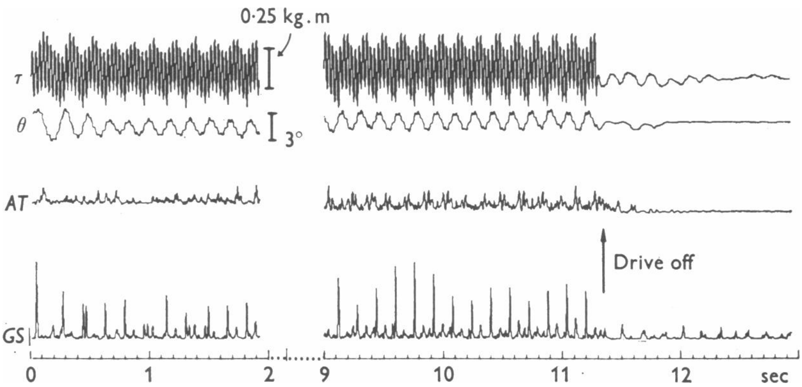

Fig. 5. Driven oscillation of the foot at 31·25 Hz. The first 1·5 sec show the start of the oscillation and then at right, the motor drive is stopped after 11 sec. The mean clonus frequency is 6·25 Hz. The motor drive was 0·6 + 0·6 sin ωt. The gastrocnemius–soleus muscles were tonically active producing an average torque of about 0·24 kg.m. (Subject N.I.R.).

because the sampling time interval was 4 msec for the angular rotation and the torque) for a 10 sec data record. The number of cycles in the averaged response increased with the frequency of the drive and is roughly equal to five times the drive frequency. Fig. 6 shows two-cycle averaged responses at nine drive frequencies. These define the average wave shape for the motor torque, the angular rotation, and the two e.m.g.s. The motor drive was 0·5 + 0·4 sin ωt volts which required tonic contraction of the gastrocnemius–soleus muscles to counteract the torque motor bias. Note that the scales in various parts of this figure are different.

As the drive frequency changes in this experiment from 3 to 31·25 Hz, the amplitude of the motor torque passes through a minimum and the angular rotation through a maximum around 6·5 Hz. This is the 'resonant frequency'. The phase lag of the angular rotation with respect to the applied torque is a small negative value of −20° to −30° at frequencies below 6 Hz, and it changes rapidly between 6·25 and 7 Hz near the resonance. The phase lag at frequencies above 7 Hz is near −160° to −180°. This phase angle change is quite rapid near the resonance as shown later in Fig. 9 *B*.

The angular rotation is nearly sinusoidal at all frequencies up to 8 Hz. The non-sinusoidal responses appear from 8 to 12 Hz. The non-sinusoidal

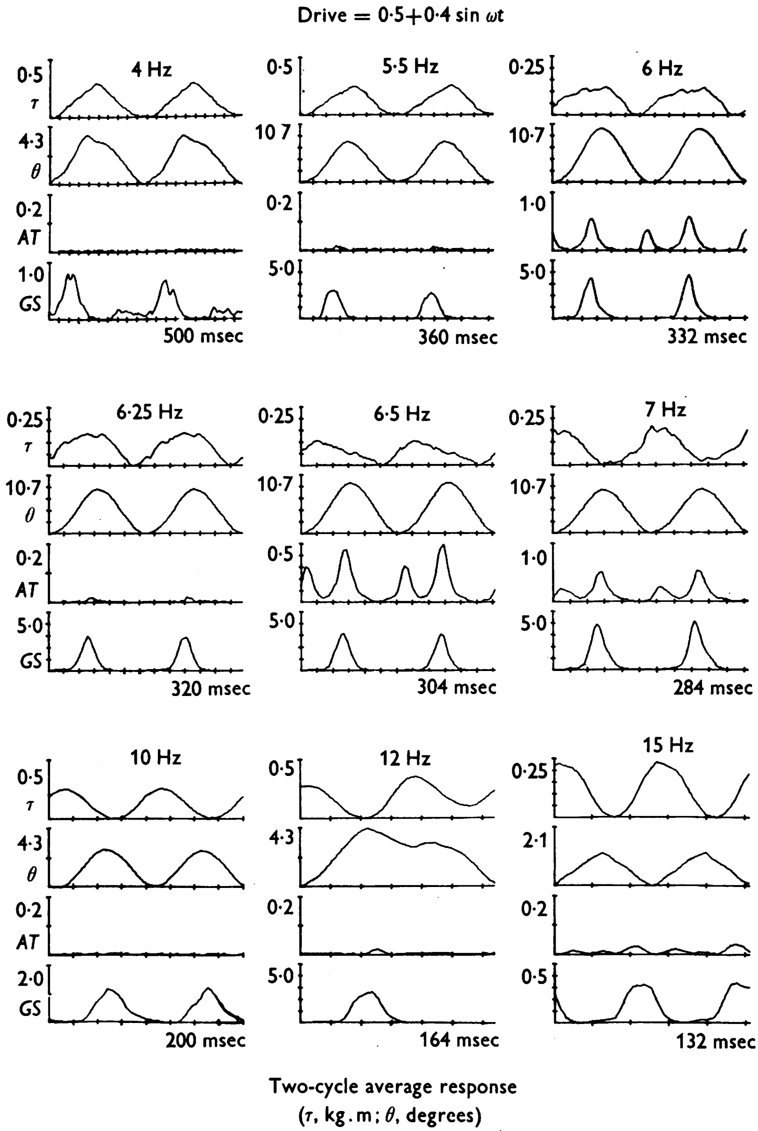

Fig. 6. Imposed sinusoidal rotation about the ankle joint. Figure shows the two-cycle averaged responses at nine drive frequencies out of twenty in this experiment. The four traces from top to bottom in each part are torque (τ), in kg.m, foot angle (θ) in degrees, rectified and filtered e.m.g. from the anterior tibial (*AT*) and the gastrocnemius–soleus muscle (*GS*). Note the scale changes in the average plots. The gastrocnemius-soleus muscles were tonically active producing an average torque of about 0·2 kg.m. The time marked in milliseconds is for two-cycles plotted. The time markers are 25 msec apart. (Subject G.C.A.)

nature of the rotation at 12 Hz drive is quite evident in the averaged response in Fig. 6, which is obtained from the first 10 sec of the data record in Fig. 3. The averaged response at 10 Hz drive, on the other hand, shows a nearly sinusoidal rotation contrary to what was shown earlier in

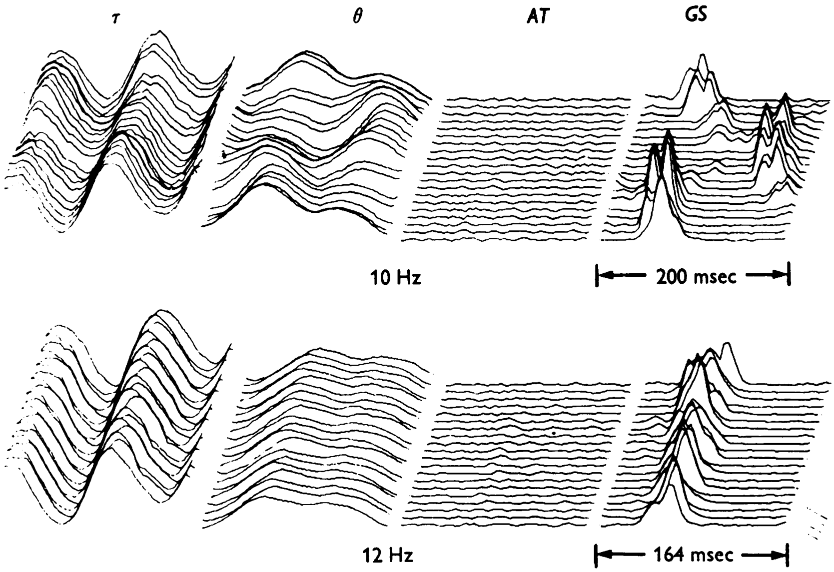

Fig. 7. The two-cycle ensemble plot of the system response at 10 and 12 Hz drive. The time axis is twice the modulation period in each case and the time is indicated in milliseconds. The average of this data is shown in Fig. 6. (Subject G.C.A.)

Fig. 4. The situation becomes clearer in an ensemble plot shown in Fig. 7. In this figure, successive two-cycle pairs are plotted from foreground to background using a pseudo three-dimensional plot. Forty consecutive cycles of the response to 10 and 12 Hz drive frequencies are shown. At 12 Hz drive, alternate torque cycles are seen to be ineffective in stretching the gastrocnemius–soleus muscle and, therefore, in producing any e.m.g. response. At 10 Hz drive, the reflex system is at a boundary between linear and non-linear modes of behaviour. This is reflected in the sudden shifting of the effective stretch cycles from the odd cycles (left side) to the even ones (right side) and back again. Averaging of such a data produces a result which appears nearly symmetric.

The e.m.g. averages in Fig. 6 show a rhythmic activity in the soleus muscle. As the frequency increases from 4 to 6 Hz, the amplitude of the soleus e.m.g. increases by nearly a factor of 5. Part of this increase may be due to the increased oscillation amplitude (a factor of 2·5). The remaining factor of 2 may be due to motor unit synchronization.

At low frequencies (5·5 Hz and below) the anterior tibial muscle shows no significant e.m.g. activity in this experiment. Near resonance, however, both the soleus and the anterior tibial muscles are rhythmically active at drive frequencies of 6·0, 6·5, 6·75 and 7·0 Hz. No activity in the anterior

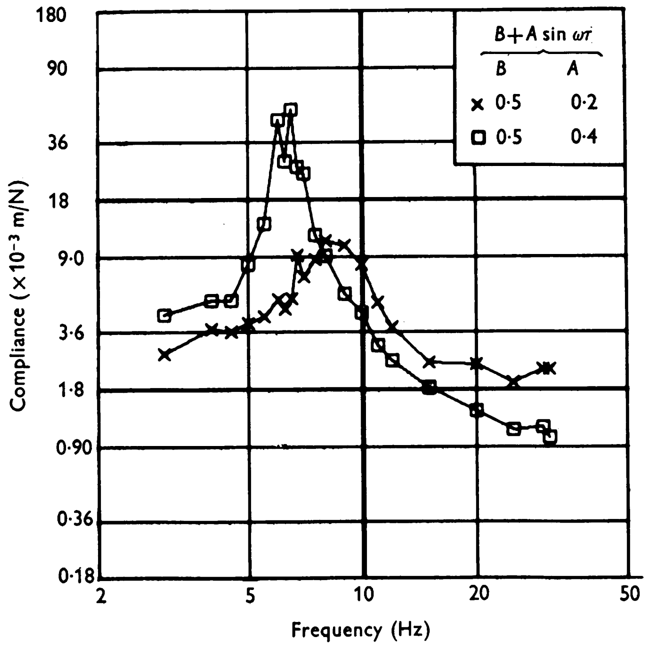

Fig. 8. Effective compliance in metres/newton as a function of the drive frequency. The motor bias voltage was kept constant at 0·5 V. The amplitude of the modulation signal for the two cases was 0·2 (×) and 0·4 (□) volts. The gastrocnemius–soleus muscle was tonically active against the motor bias producing an average torque of about 0·2 kg.m to maintain the zero angular foot position. The 0·4 V curve is computed from the data shown in Fig. 6. (Subject G.C.A.)

tibial is observed at 6·25 Hz drive frequency and at drive frequencies of 7·5 Hz and above. At 6 and 6·5 Hz, co-activation of the anterior tibial and the soleus muscles is apparent. Near the resonant frequency, the co-activated gastrocnemius–soleus and anterior tibial muscle e.m.g. peaks occur about 65 msec after the start of the dorsal stretch. A smaller peak in the anterior tibial muscle e.m.g. occurs about 80 msec after the start of plantar stretch.

In a linear, constant parameter system, the output of the system will show only those harmonic components which are present in its input. Figs. 3, 4 and 6 clearly indicate distortion from linear response. Fourier transform analysis of this data shows that a significant percentage of the power in the angular rotation signal (up to 80 %) is present in subharmonic frequencies over the narrow range of drive frequencies between 8 and 12 Hz (Agarwal & Gottlieb, 1975*a*).

Fig. 8 shows the effective system compliance for two levels of modula-

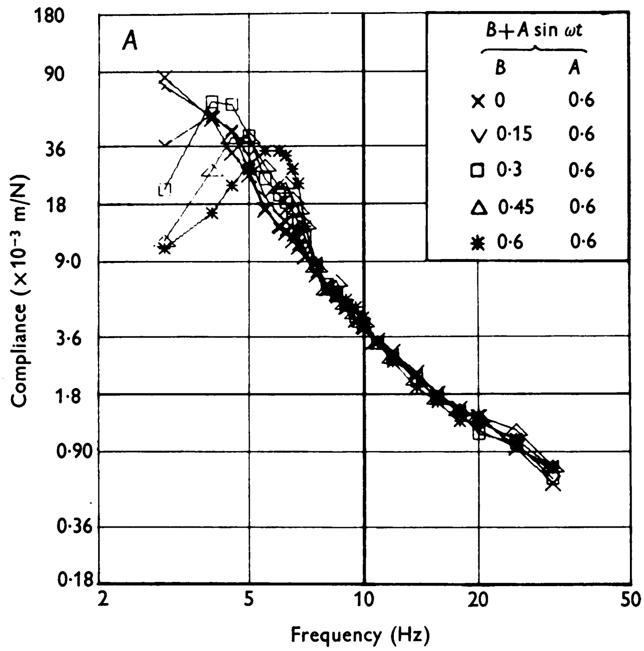

Fig. 9a. For legend see facing page.

tion amplitude. The experiment at 0·4 V modulation is the same as shown in Fig. 6. Two peaks are observed at 6 and 6·5 Hz. At 6·25 Hz the anterior tibial muscle e.m.g. was silent (Fig. 6) and the compliance was significantly smaller than at the two adjacent frequencies tested. At 0·5 V modulation (not shown), the compliance curve was similar to the one for 0·4 modulation except that only one peak was seen at 6·25 Hz. The smaller amplitude modulation (0·2 V) response differs in two significant ways. First, the compliance at low frequencies is smaller (the joint appears stiffer) and second, the resonant frequency is near 8 Hz. With the bias torque requiring tonic soleus contraction, low-frequency compliance and the resonant frequency depend upon the amplitude of modulation. At low frequencies, the increase in compliance is monotonic with increased modulation. The resonant frequency is near 8 Hz at low modulations and decreases to about 6·5 Hz as the modulation amplitude is increased.

Fig. 9 shows the effective compliance of the system and the corresponding phase angles between the angular rotation and the motor torque (rotation lagging the torque) for another subject. In this sequence, the modulation amplitude was constant and different motor bias voltages, from 0 to 0·6 V, which required tonic gastrocnemius–soleus muscle activity were used. The bias torque was in the range from 0 to 0·24 kg.m.

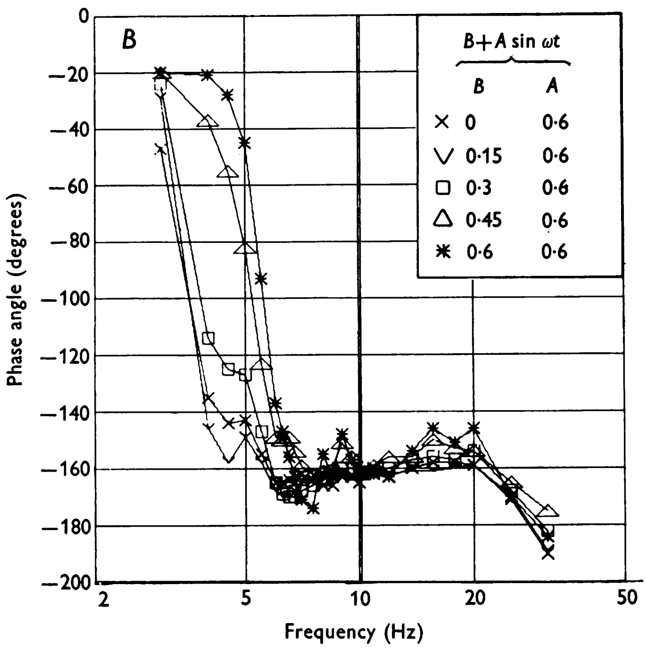

Fig. 9. Effective compliance and the phase angle between the motor torque and the angular rotation as a function of the input frequency for different levels of bias torque. The amplitude of the modulation signal to the motor was kept constant at 0·6 V. The motor bias voltages for the five cases were 0, 0·15, 0·3, 0·45 and 0·6 V. For the positive non-zero bias the gastrocnemius–soleus muscle was tonically active producing an average torque proportional to the bias voltage ranging from 0 to 0·24 kg.m to maintain the zero angular foot position. The angular rotation lags the applied torque. The sudden increase in the phase lag indicates the occurrence of resonance. A second break in the phase angle near 20 Hz is an indication of higher order system dynamics. (Subject N.I.R.)

This is only a small percentage of the total work capacity of the gastrocnemius–soleus muscles which is estimated to be over 16 kg.m (Brunnstrom, 1972). With the modulation constant, the resonant frequency monotonically shifts to higher values with increasing bias (increasing tonic activity in the soleus muscle). This is consistent with increasing muscle stiffness due to activation. The phase lag changes rapidly near the resonance. Although the compliance curve for zero bias does not show a resonance (3 Hz was the lowest frequency tested), a resonance near 3 Hz is indicated by the sharp increase in phase lag from 3 to 4 Hz.

Fig. 10 shows two experiments. (These data were obtained using the torque feed-back servomechanism as indicated in Methods.) In the first experiment, the compliance was measured in both the left and right legs of the

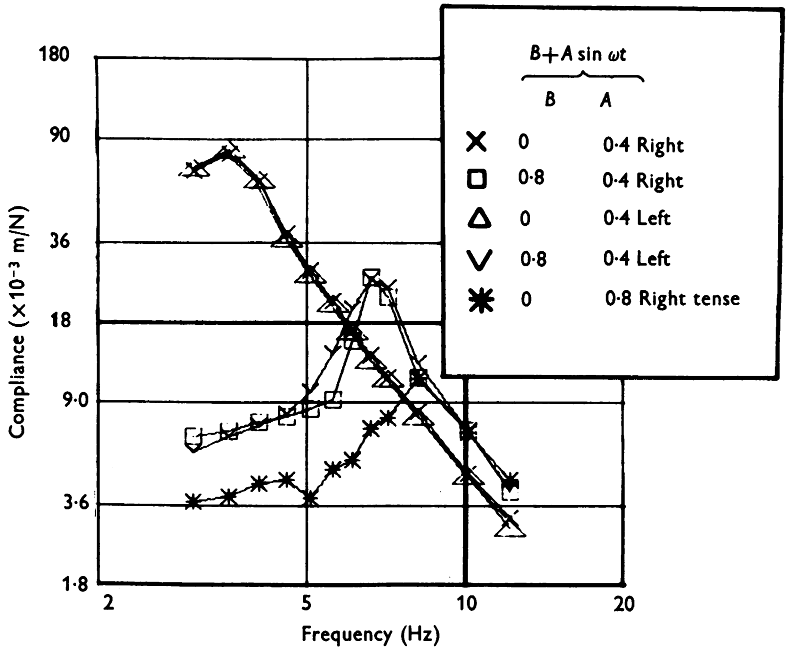

Fig. 10. Effective compliance as a function of the input frequency from two types of experiments. As noted in the Methods these data were obtained using a torque feed-back servomechanism. ×, △, compliance of the right and the left leg respectively when the muscles were relaxed. □, V, compliance of the right and the left leg when the soleus was tonically active. *, compliance when the subject was asked to make his leg tense (right leg) which required using both the gastrocnemius-soleus and anterior tibial muscles. (Subject G.L.G.)

subject under conditions of relaxation (zero bias voltage) and tonic soleus activity. The curves from the two limbs are virtually identical. In the second experiment (* points), the subject was asked to tense both gastrocnemius–soleus and anterior tibial muscle groups to stiffen the limb as much as possible. The resulting rotation was smaller under these conditions than when only one of the muscle groups was active. The resonance is observed at 8 Hz.

In a few experiments, the effective compliance was measured with tonic anterior tibial contraction. The same resonance phenomenon is seen in the 5–8 Hz range but we have not observed either clonus or the non-sinusoidal type of responses seen in Figs. 3 and 4.

In one experiment the motor drive was continued for 90 sec at 6·75 Hz (B = 0·5 V and A = 0·5 V). When the modulation voltage of the motor was turned off, self-sustained oscillation of the foot continued for nearly 60 sec, at which time the subject voluntarily halted it. In this experiment, the anterior tibial muscle showed no activity during driven or self-sustained oscillations. The self-sustained oscillations were at a slightly lower frequency than the original drive (6·35 Hz frequency as measured from the Fourier transform analysis). The oscillation was generated by the soleus reflex loop alone and did not visibly involve the antagonist muscle. This is also true for the self-sustained oscillations shown in Fig. 4 between 12 and 15 sec marks.

DISCUSSION

The resonant frequency

Mechanical and neural mechanisms can both contribute to the resonance phenomenon. If a limb behaves as a passive mechanical system with negligible stretch reflex activity, it may be mathematically modelled to a first approximation by a second order differential equation consisting of the mechanical parameters: J (moment of inertia), D (viscous coefficient) and K (spring stiffness) (see Methods). Such a system when underdamped exhibits a resonant frequency which is a function of the ratio K/J. In a relaxed limb, the absence of phasic synchronized e.m.g. activity indicates that the stretch reflex does not significantly contribute in driven oscillation; the joint then has a resonant frequency around 3–4 Hz (Figs. 9 and 10).

Muscle activity affects the resonant frequency in two ways: muscle stiffness (K) increases (Wilkie, 1950), and stretch reflex mechanisms become more sensitive. By choosing appropriate oscillation amplitudes, one can demonstrate the different effects of increased muscle stiffness and of the stretch reflex contribution.

In experiments using small driving torques, little or no phasic e.m.g. was evident in the averaged response. In such cases, the resonant frequency increased with the level of tonic muscle contraction. Fig. 8 shows a case of 8 Hz resonance with a modulation amplitude of 0·2 V.

The absence of a large phasic e.m.g. response should not be taken to contradict the observation that muscle spindles are exquisitely sensitive to small amplitude sinusoidal stretching (Matthews & Stein, 1969), at least in decerebrate cats. The e.m.g., however, indicates that little synchronous activation of motor units was taking place, and whatever contribution the phasic stretch reflex may have made to the resonance could not be great. The dominant factors in such cases were the elastic compliance of the muscles and the inertia of the moving parts.

The contribution of the muscle spindles and the stretch reflex became significant when there was tonic muscle activity and the amplitude of driven oscillation was larger. A resonance then appeared between 5 and 7 Hz, a frequency significantly different than in the relaxed limb and also different from that in the tonically active limb with low modulation drive.

With tonic soleus muscle activation and with sufficient stretch, the muscle spindles respond with a volley which probably occurs in the early part of the stretch phase (Hagbarth, Wallin & Lofstedt, 1975). This would produce a reflex e.m.g. discharge some 50–55 msec later and a significant muscle contraction about 100 msec after the start of the stretch. During 6·25 Hz driving, soleus stretch reflex contraction would coincide with the plantar phase of the torque motor. Thus, motor torque and active muscle contractile torque would be in the same direction and produce a larger rotation for any given degree of motor torque. The resulting increase in the amplitude of oscillation is gradual as seen in Fig. 2, and this contributes to the resonance in the system.

With a constant amplitude of driving torque, increasing tonic muscle activation produced a monotonic increase in the frequency of resonance up to about 6·5 Hz (Fig. 9), a consequence of increasing muscle stiffness. At about 6·5 Hz the stretch reflex component dominated. When the subject was asked to tense his leg, the compliance was considerably reduced (Fig. 10) and the resonant frequency increased to near 8 Hz.

The increase in compliance, which occurs at low frequencies as the amplitude of the driving torque is increased, is possibly of muscular rather than reflex origin. At low frequencies, any reflex activation of the muscle should reduce its compliance in rough proportion to the amplitude of activation. If the non-linear, concave downwards shape of the static muscle length–tension curve applies also under dynamic conditions, an increase in compliance might be produced at mean values of muscle length just below the peak of the curve.

Phase relationship

The angular rotation always lags the motor torque over the entire frequency range studied. The phase angle changes sharply near the resonance and the curves of Fig. 9 are compatible with a typical second order system response. (Although the phase angle data indicate another break frequency near 20 Hz.)

In the literature it is customary to measure the phase relationship between the stretch and the e.m.g. response (Burke *et al.* 1971; Westbury

1971). These are extensions of similar definitions used in muscle spindle work (Poppele & Bowman, 1970). In these and many similar studies, the phase relation is defined with respect to the peak point of the stretch. Westbury (1971), recording from the cat's motoneurones, observed the peak of the excitory post-synaptic potential to be about 90° (occasionally as much as 150°) before the peak of the applied stretch at frequencies of 5 Hz or more. Jansen & Rack (1966), studying the stretch reflex of the soleus muscle of the decerebrate cat, showed that the phase lead of the peak e.m.g. relative to the peak length often reached and sometimes exceeded 90°. The maximum phase advance occurred at about 4 Hz (see also Poppele & Terzuolo, 1968).

In human subjects the neural transmission for the Hoffmann reflex is of the order of 35 msec, and for the soleus stretch reflex it is of the order of 50 msec. At 6 Hz, the lag introduced by a 50 msec conduction delay is about 110°. Since it is not clear which part of the stretch is most effective in producing the spindle activity, the measurement of the phase relationship with respect to the peak stretch may be misleading.

From the data shown in Fig. 6 and similar experiments with modulation voltages of 0·5 and 0·6 V for the same subject, we have estimated the time of the occurrence of the peak of the averaged soleus e.m.g. response (full-wave rectified and filtered) from the start of the stretch cycle to be as follows:

Frequencies	Time for peak e.m.g. value
4–5·5 Hz	58 msec (S.D. = 8·0 msec)
6–7 Hz	64 msec (S.D. = 1·5 msec)
7·5–12 Hz	67 msec (S.D. = 6·4 msec)
15–31·2 Hz	52 msec (S.D. = 2·7 msec)

Rack & Ross (1975) have reported averaged e.m.g. responses of the human biceps during imposed sinusoidal movement of the elbow joint. No time estimates were given. There was more variability in the time-to-peak of the e.m.g. at frequencies between 4 and 5·5 Hz than between 6 and 7 Hz where the amplitudes of oscillation were larger. It is likely that spindle activity was then greater and more synchronized and consequently produced a more synchronized reflex e.m.g. volley. The increased average value of 64 msec as compared to 58 msec at lower frequencies may be due in part to the activation of the anterior tibial muscle before the soleus activity (Fig. 6) and reciprocal inhibition within the spinal cord. In the higher frequency range from 7·5 to 12 Hz, the increased mean and standard deviation values for time-to-peak e.m.g. result from the non-sinusoidal nature of the rotational response.

In this subject, a quick dorsiflexion of the foot by the motor produces a reflex e.m.g. response starting at 44 msec and ending at 58 msec. The peak of the rectified, filtered reflex e.m.g. occurs at about 55 msec. The latencies measured from the beginning of extension during sinusoidal oscillation above 12 Hz are thus very close to this stretch reflex latency. At no frequency is the response directly related in time sequence to either the peak stretch or the peak velocity.

Interaction with physiological tremor

Physiological tremor in human subjects occurs between 8 and 12 Hz. Many investigators have observed 8–12 Hz bursts of motor unit activity in surface and needle e.m.g. recordings from a variety of skeletal muscle during steady voluntary contractions. It is during such contractions that an 8–12 Hz physiological tremor has been recorded from the extended third digit (Halliday & Redfearn, 1956; Lippold, 1970), the partially flexed forearm (Fox & Randall, 1970), the abducted index finger (Stephens & Taylor, 1974), and the soleus during quiet standing (Lippold *et al.* 1958; Mori, 1973). Mori (1973) has found a tendency toward synchronization of contiguous motor units in the soleus during quiet standing and found motor units to fire synchronously at about 9 spikes/sec. Elble & Randall (1976), recording from the *extensor digitorum*, suggested that the 8–12 Hz component of finger tremor is not simply the consequence of synchronization of motor unit firing at 8–12 spikes/sec. Rather, motor units firing at 13–22 spikes/sec contribute to the physiological tremor as a result of grouped discharges within a simple motor unit spike trains, i.e. entrainment of the motor units (Mori, 1975).

The 8 Hz resonent frequency observed with tonic muscle activity and low amplitude drive falls within the range of the physiological tremor. It is possible that the same mechanisms responsible for tremor are also responsible for this resonance. The hypothesis that physiological tremor is produced by the stretch-reflex servo (Lippold, 1970) seems to be contradicted by our finding that the dominant resonant frequency of the closed loop system under moderately driven oscillations is around 6 Hz. However, there may be more than one mechanism responsible for resonance at different resonant frequencies. The 6 Hz frequency is associated with a strong stretch reflex component. The contribution of the stretch reflex to the 8 Hz resonance seen with smaller stretches is not clear. The system could be operating in one of two modes depending on the bias torque and the amplitude of oscillation. The mode of operation would depend on the sensitivity of the muscle receptors and the gain of the reflex arc.

Progressive increases in oscillation amplitude

The slow build up in amplitude of the response during oscillation near the resonant frequency in Fig. 2 is a common phenomenon in non-linear systems (Cunningham, 1958; Gibson, 1963). However, in the ankle the amplitude cannot grow beyond certain limits due to increased elastic joint stiffness at large angles and possibly increased muscle viscous resistance at large velocities of stretch. The 'jump' phenomenon (an abrupt change in the output amplitude as the input frequency increases) reported by Walsh (1975*a*, *b*) near the resonant frequency of the wrist movement is also commonly seen in mechanical systems with mass, damping and a spring whose stiffness increases with stretch (Cunningham, 1958). Such a situation could arise in the motor system where the stretch produces a reflex muscle activation which increases muscle stiffness. For the human arm, the compliance varies from $0{\cdot}5 \times 10^{-3}$ to $1{\cdot}5 \times 10^{-3}$ m/N (derived in Gottlieb, Agarwal & Stark, 1969 from Wilkie, 1950).

Non-sinusoidal oscillation

A number of mechanisms can contribute to the generation of non-sinusoidal oscillations seen in the 8–12 Hz drive range. From an analytical viewpoint, we have two coupled dynamic systems. One is the drive motor which is oscillating at 8–12 Hz. The other is the neuromuscular mechanism of the foot which is resonant at approximately half that frequency. During the 'non-linear' intervals, we are observing beating (Walsh, 1971) between the two systems with a resultant dominant harmonic in the response being the difference between the two frequencies. Because the relationship between the two frequencies is only approximately 2:1, there is drift in their relative phase relationship and sudden jumps from beating to non-beating such as seen in Fig. 4. These two modes of behaviour alternate. In most subjects, there is some drive frequency at which the non-linear response is observed to be uninterrupted, presumably because of an exact 2:1 relationship between the motor drive frequency and the neuromuscular system resonance (12 Hz drive shown in Fig. 3).

A physiological explanation can be offered based on the properties of the stretch reflex and muscle contraction. Spindle stretch produces a reflex activation of the muscle and an e.m.g. response about 55 msec after the start of the stretch. Peak twitch contraction develops in the soleus muscle about 75 msec after the e.m.g. volley (Buchthal & Schmalbruch, 1970). With a 10 Hz drive, successive stretches are 100 msec apart. The reflex contraction produced by one stretch cycle overlaps with the stretching phase of the next cycle. Muscle contraction in the second cycle, in response to stretch in the first cycle, opposes the motor torque and, therefore, the net torque available to stretch the muscle is reduced. This activation of the muscle also increases its stiffness requiring a larger force for the same amount of stretch. Therefore, this second cycle will produce a smaller stretch and smaller reflex response. The third cycle will then be unopposed and be a repeat of the first.

The non-sinusoidal responses observed between 8–12 Hz drive may be due to interaction of the motor system with mechanisms responsible for physiological tremor. Such non-sinusoidal responses were not observed by Joyce *et al.* (1974) because with a displacement drive, every cycle of stretch is the same.

The non-sinusoidal response is frequently observed if the gastrocnemius–soleus muscle is tonically active. We have not observed it when the anterior tibial muscle is tonically active. The synchronization of the motor units seen in the soleus and not in the anterior tibial muscle (Mori, 1973, 1975) may account for this difference.

Self-sustained oscillations

Prolonged motor-driven oscillation of the foot (60 sec or more) at frequencies near resonance with soleus tonically active against the motor bias is very fatiguing to the soleus muscle and in this condition, we frequently observed self-sustained oscillations when the drive was turned off. Alternating activation of the antagonistic muscle pair is not necessary to maintain such oscillations. This phenomenon was predicted by Joyce *et al.* (1974) and appears to be closely related to the pathological clonus. As little as 10 sec of conditioning oscillation is often sufficient, however, to create a favourable state of spinal excitability.

It is impossible to precisely localize the origin of this phenomenon. The many receptors excited by sinusoidal movement may produce an array of effects involving the whole central neuro-axis. Surguladze & Gurfinkel (1973) observed rhythmic changes in the excitability of spinal motoneurones for a briefer period (500–600 msec) after arrest of voluntary, rhythmic movements.

Post-tetanic potentiation of the myotatic reflex in man is known to last for 30–40 sec (Hagbarth, 1962). A heightened state of excitability of the reflex arc due to sinusoidal stretching in a fatigued muscle might be the result of such a mechanism. However, the immediate clonic activity seen in a subject with 31·25 Hz drive (Fig. 5) suggests that the rhythmic stretching evokes long-loop, supraspinal reflexes which increase spinal excitability and produce clonus. Marsden, Merton & Morton (1976), studying the human flexor pollicis longus muscle, have hypothesized an increase in the reflex arc gain in the fatigued muscle. Such an increase could make the closed loop system unstable. Matthews (1966) observed in decerebrate cats that when there was a tonic activity in a muscle before vibration was applied, a slightly greater active tension was produced which often persisted for a few seconds after the vibration and in two experiments lasted for 10 sec or more. He suggested that the afferent discharge set up by the vibration had prolonged central excitatory actions in addition to its direct excitation of soleus motoneurones by short spinal pathways.

System complexity

Unlike a passive mechanical system, the resonance phenomenon at the ankle joint is complicated by changes in the parameters of the muscle (stiffness and viscosity) which depend on the degree of muscle activation, muscle length and the velocity of movement, on changes in the response characteristics of the muscle receptors (particularly co-activation of the fusimotor neurones) and on changes in the excitability of the spinal cord motoneurone and interneurone pools. Experimental selection of the appropriate level of tonic activity and amplitudes of oscillation, causes different resonant modes to be excited. A lumped parameter, linear analysis of such a system is likely to be of limited use, although this approach has frequently been used to advance the servo-hypothesis of physiological tremor with insufficient regard to the system resonant frequencies measured with external inputs.

The system instability (clonus and progressive increases in amplitude of oscillation) observed in these experiments is of significant interest because it implies system dynamics (for a linear system) which are drastically different from those predicted by the normal behaviour observed using a tendon jerk input.

Conservative engineering design tends to emphasize stability and this normally characterizes our view of most physiological regulating mechanisms. An alternate view of many such regulators is that they may be inherently unstable within some of their inner loops. Homoeostasis is preserved, however, by the existence of outer loops which become active when some of the state variables approach the boundaries of some allowable 'state space'. Thus, the inherent instability is only observed in pathological conditions or perhaps in experiments such as those described here. Certainly, none of our subjects has any history of neuromuscular illness nor have they any present complaints. None show ankle tremor and none have difficulty walking or driving, but eight of ten have experimentally demonstrated clonus. This is a most interesting paradox. The fact that such a state can be produced by a simple, rhythmic, mechanical stimulus is of importance because such stimuli arise from many forms of vibrating machinery (Wasserman & Badger, 1973).

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