

FORCED OSCILLATIONS OF THE ANKLE JOINT*

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ABSTRACT

The results of a study using low frequency vibration (3 to 30 Hz) applied to the human ankle joint are discussed. Results indicate, in part, self-sustaining oscillations of the fatigued ankle joint near the resonant frequency after the vibratory stimulus had been removed and after slowly increasing amplitude of oscillation at frequencies near resonance.

INTRODUCTION

There has been a growing concern in recent years regarding the effects of vibration upon human operators. Nearly everyone is exposed at one time or another to some form of vibration, and it is conservatively estimated that there are eight million workers exposed to some form of industrial vibration in the United States alone.¹ Wasserman and Badger² have compiled a bibliography of the literature on the effects of vibration.

There are essentially two forms of vibration of interest. The first, called whole body vibration, is the application of vibration, usually to the entire body, from head to toe as from a vibrating floor. The second, called segmental vibration, is the application of vibration to specific body parts such as the hands from vibrating hand tools.

Long term exposures to vibration in workers produce many pathological syndromes.^{2,3} Our knowledge of the direct effects of vibration on the human motor system is very limited. Vibration is a potent stimulus to the muscle spindles⁴⁻⁶ and, therefore, is potentially capable of producing significant changes in the control and coordination of movements.

Vibration in the frequency range of 50 to 200 Hz applied directly to the muscle belly or muscle tendon of the gastrocnemius-soleus muscle produces the tonic vibration reflex and significantly influences the tendon-jerk and Hoffmann reflexes.⁷⁻¹¹ Recent studies have shown kinaesthetic illusions arising from the stimulation of intramuscular receptors by vibration at 100 Hz with a physiotherapy vibrator.^{12,13}

In this paper, we will examine the effects of low frequency (3-30 Hz) forced oscillation of the ankle

joint. The moment of inertia of the limb presents an inertial load to an applied torque, the muscles offer a visco-elastic resistance to lengthening, and in addition to these, movement may 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 fairly constant. The resistance of muscles to lengthening and the intensity of the stretch reflexes are dependent on the force of contraction.

Joyce, Rack, and Ross¹⁴ have studied the forced oscillations of the human elbow joint. Many of their results were similar to those reported here. However, they did not study single frequencies, and the total frequency range up to 22 Hz was scanned in less than 30 seconds. Berthoz and Metral¹⁵ and Neilson¹⁶ have used similar techniques of applying a sinusoidally varying force while measuring elbow position. Walsh^{17,18} applied sinusoidally varying forces to the wrist and has observed resonance and jump phenomenon. He scanned the total frequency range up to 15 Hz in 10 seconds. The results to be presented here show that these frequency scanning techniques fail to reveal a number of interesting behavioral phenomena.

METHODS

Experiments were done on six normal human subjects. The subject sat in a chair with his right foot strapped to a foot-plate which permitted only dorsiflexion-plantarflexion about the ankle joint. A schematic of the equipment used is shown in Figure 1.

The plate is rotated by a D.C. torque motor via a gearbelt and pulley system for torque amplification. Constant tension springs (not shown in the figure) are also used to balance the downward gravitational force on the foot. With the motor off and the subject completely relaxed, the resulting joint position

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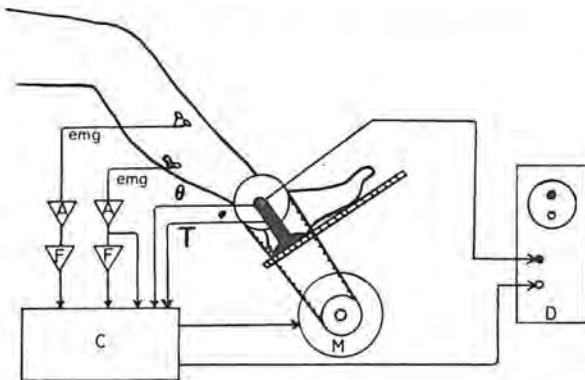


Figure 1. A schematic of the apparatus used for the forced oscillations of the ankle joint. The components are: D. C. Torque Motor (M) driven by a Bulova power amplifier, electromyogram is recorded using disc surface electrodes placed over the bellies of the soleus and anterior tibial muscles, EMG amplifiers (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 SPC-16.

(approximately 90° between the foot and the tibia) is defined as the zero angular position, and this reference is provided as a fixed dot on a dual beam oscilloscope. The second beam is used to display the subject's true angular position.

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 position.

The torque was measured by four strain gauges on the side arms of the footplate connected in a bridge circuit. The angular rotation was measured by a continuous potentiometer. Electromyograms (EMG) were recorded from disc surface electrodes placed over the bellies of the soleus (GS) and anterior tibial (AT) muscles. These were amplified, full-wave rectified, and filtered before recording.^{19,20}

Sinusoidal signals were superimposed on the mean torque level. Frequencies from 3 to 30 Hz were used. In some experiments, frequencies down to 1 Hz were used. The torque, the resulting angular rotation, and the electromyograms were continuously recorded on a digital tape. The angle and the torque signals were sampled at a rate of 250 Hz and the filtered EMG's, at a rate of 500 Hz. The data were continuously recorded for 10 seconds or more at each frequency. After 10 seconds, we frequently recorded the data going through a stop, start, and stop again of the modulating signal. The bias voltage was constant throughout the run. This allowed us to observe self-generated oscillations as discussed in the results section.

Whereas the applied torque signal was nearly a single frequency sinusoid, the angular rotation at

certain frequencies had significant distortion. For this reason, the following analyses were done:

1. Fourier coefficients at the fundamental frequency were obtained from the torque, the angular rotation, and the EMG data for the first 10 seconds. The analysis was done for 20 half-second data records, and the resulting numbers were averaged.
2. A two-cycle time average was generated for a 10-second data record by taking successive intervals equal to twice the modulation period.
3. An average Fourier transform was obtained by using five 2.048-second (512 points) data records with the incremental resolution frequency of 0.4883 Hz.

In some experiments, oscillation near the resonant frequency was applied continuously for 100 seconds or more to develop muscle fatigue and to observe the self-generated oscillations after the modulating signal of the motor was stopped.

RESULTS

The two-cycle averages that define the average wave for the torque, the angular rotation, and the two EMG's are shown in Figure 2 at eight drive frequencies. The motor drive was $0.5 + 0.4 \sin \omega t$ volts that required tonic contraction of the gastrocnemius-soleus muscle to counteract the torque motor bias.

There are a number of interesting observations in these two-cycle-averaged responses. As the frequency is changed from 3 to 30 Hz, the amplitude of the measured torque (differential torque between the motor and the foot torque) passes through a minimum near 6.5 Hz and the amplitude of rotation is near maximum at these frequencies. At low frequencies, the anterior tibial muscle has no measurable EMG activity. (The constant value of AT EMG at 4 Hz was just the offset of the filtering amplifier.) Near resonance, both soleus and AT are rhythmically active. At 12 Hz, the angular rotation is significantly distorted from the sinusoidal shape. Some distortion is also present in the torque wave-form. Alternating waves of the GS EMG are nearly suppressed.

Although Figure 2 clearly points out the nonlinear nature of the system, as a first-order approximation, a linear analysis was performed. Fourier coefficients at the drive frequencies were computed and their amplitudes are given in Table 1.

The effective compliance of the muscle is defined by taking the ratios of the angular rotation and the torque Fourier coefficients. If R denotes the radius of action of the muscle, then

$$\begin{aligned} \frac{\Delta L}{\Delta F} &= \text{Effective compliance of the muscle} \\ &= 0 \times R / (\tau / R) \\ &= (\theta / \tau) R^2 \text{ meters/newton} \end{aligned}$$

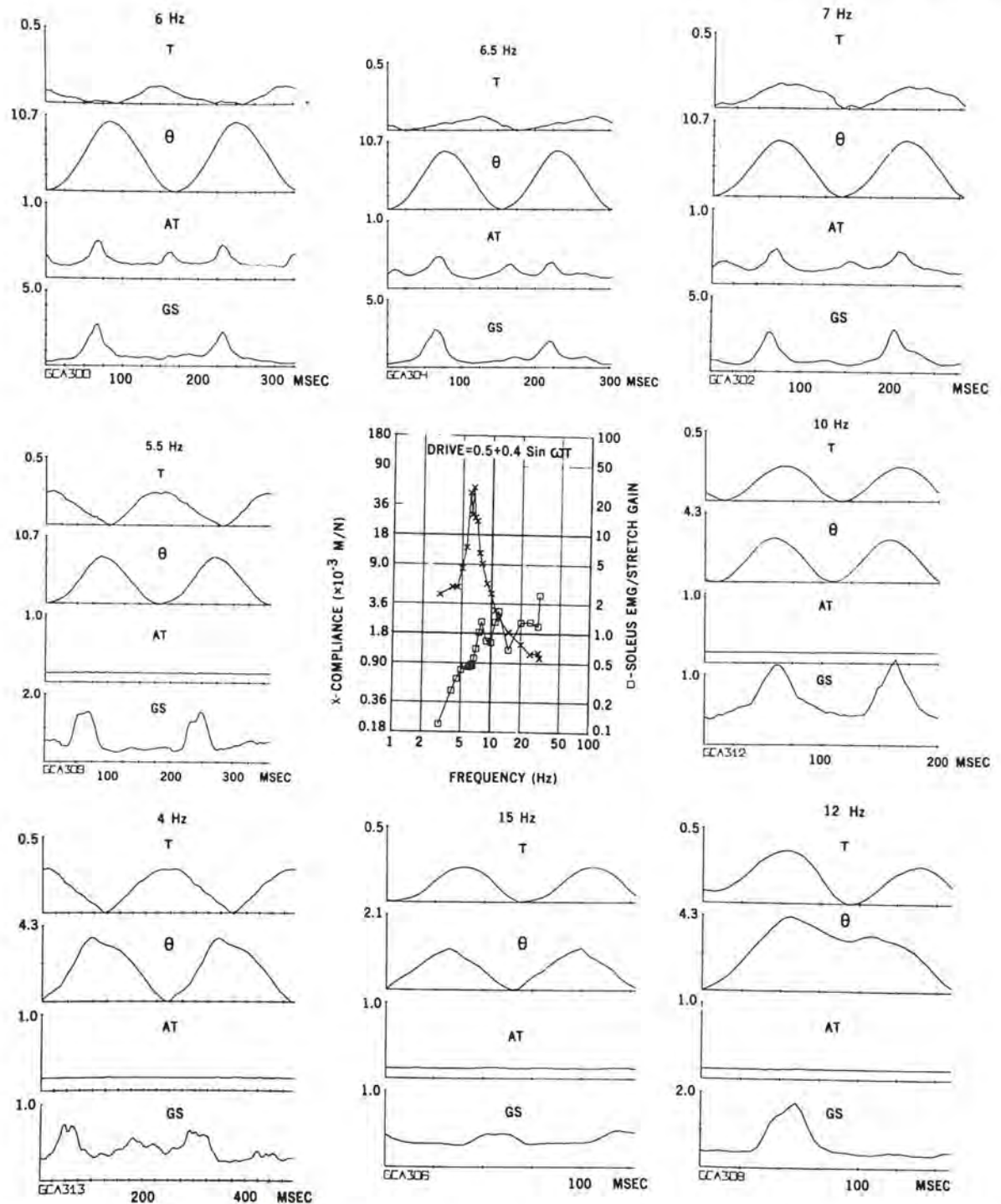


Figure 2. Imposed sinusoidal movement of the ankle joint. Figure shows the two cycle averaged response at eight drive frequencies. The four traces from top to bottom in each part are torque in kg-meters, foot angle in degrees, rectified and filtered EMG from the anterior tibial and the gastrocnemius-soleus muscles. The averaging was done for a 10 second data record by taking successive intervals equal to twice the modulation period. The motor drive was $0.5 + 0.4 \sin \omega t$. The center figure shows the effective compliance (x) in meters/newton and soleus EMG/stretch gain (□) in arbitrary units as a function of the input frequency. These were calculated from the Fourier analysis at the drive frequency. The effective lever arm of the muscles is assumed to be 5cm.

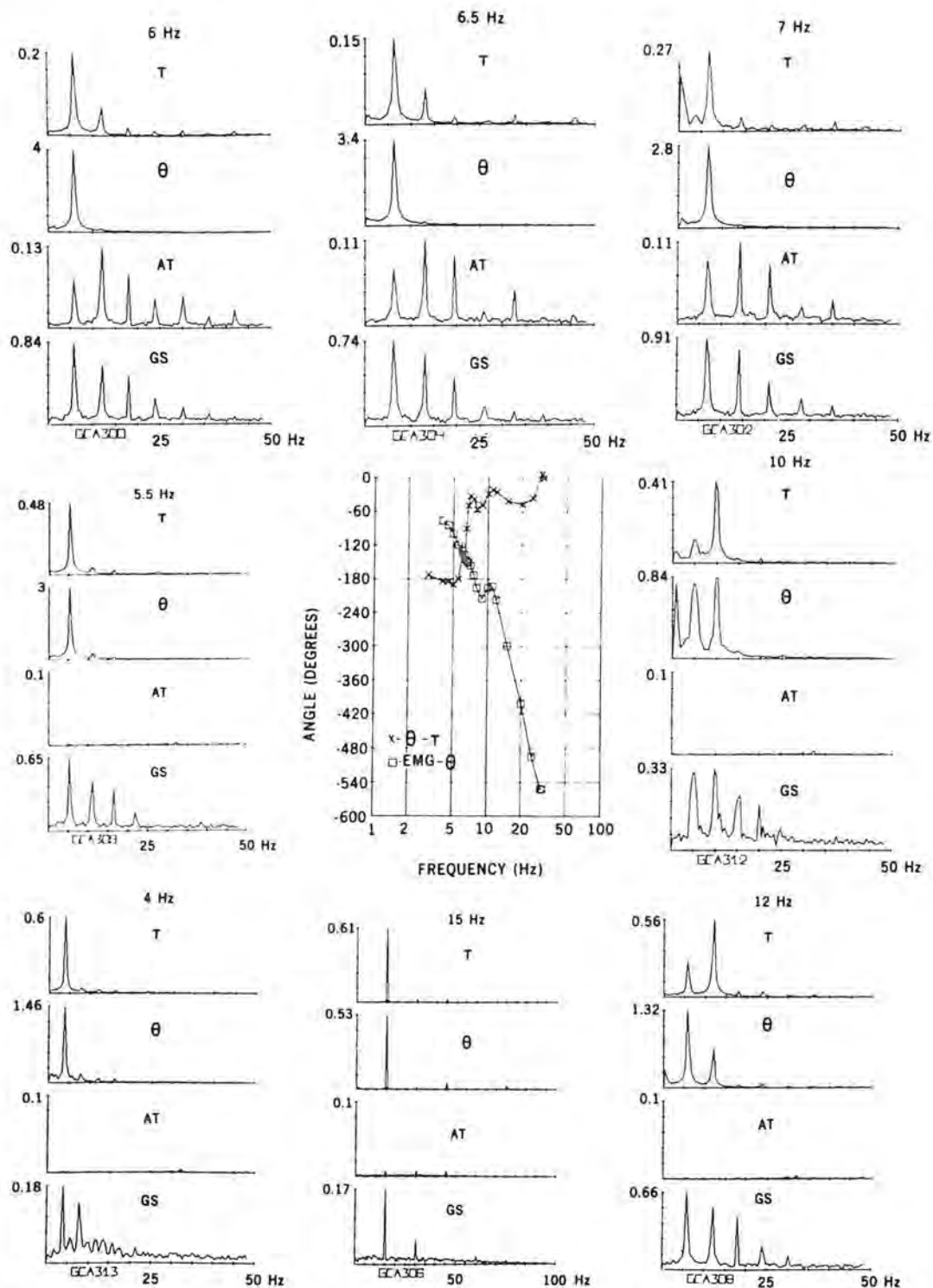


Figure 3. Imposed sinusoidal movement of the ankle joint. Figure shows the Fourier transform of the torque (Kg-meters), angular rotation (degrees) and rectified, filtered electromyogram recorded from the anterior tibial and the gastrocnemius-soleus muscles at eight driving frequencies. The motor drive was $0.5 + 0.4 \sin \omega t$. The center figure shows the phase angle between angular rotation and the applied torque (x) and between the soleus EMG and the angular rotation (\square) as a function of the drive frequency. The phase relationship was calculated from the Fourier analysis at the drive frequency.

Table 1. Fourier coefficients of the data in Figure 2*

Fre- quency, Hz	GS-EMG FC	GS-EMG DC	Rotation, deg FC	Torque, kgM FC	Torque, kgM DC	Com- pliance, (M/N) $\times 10^{-3}$
4	0.19	0.39	1.6	0.12	0.16	5.3
5	0.51	0.51	2.6	0.13	0.19	8.2
5.5	0.76	0.63	3.5	0.11	0.19	13.5
6	1.0	0.78	4.7	0.04	0.2	47.5
6.25	0.9	0.74	4.0	0.06	0.18	28.7
6.5	0.95	0.77	4.4	0.03	0.18	54.3
6.75	0.95	0.76	3.7	0.06	0.2	26.7
7	1.2	0.95	3.8	0.06	0.19	24.8
8	1.0	0.80	1.7	0.08	0.53	9.0
10	0.5	0.61	1.3	0.12	0.17	4.6
12	0.63	0.66	0.81	0.13	0.18	2.5
15	0.17	0.37	0.53	0.12	0.20	1.8
25	0.19	0.34	0.33	0.13	0.17	1.1
30	0.16	0.34	0.3	0.11	0.16	1.1

*The motor drive was $0.5 + 0.4 \sin 2\pi ft$. FC denotes the Fourier coefficient at the drive frequency, and DC is the average value. Numbers have been rounded to two digits.

where the angular rotation θ is in radians and torque τ is in newton-meters. For plantar as well as for dorsal movements, the radius of action R is roughly 5 cm, although it varied slightly with the foot angle.²¹

The center of Figure 2 shows the effective compliance as a function of the drive frequency. Also shown is the soleus EMG/stretch gain.

Figure 3 shows the Fourier transforms of the same data. The distortion of the angular rotation at 10 and 12 Hz is manifested by subharmonic components. The center of Figure 3 shows the phase angles between the angular rotation and torque and between the soleus EMG and the angular rotation. The sudden change in phase at 6.5 Hz in the θ - τ curve is indicative of the resonance at that frequency. The EMG- θ phase can be accounted for by a neural transport delay of about 55 msec.

Figure 4 shows the slowly increasing amplitudes of oscillation when modulation is turned on near the resonant frequency of 6.5 Hz. The peak EMG of the gastrocnemius-soleus muscle also increases in amplitude as the oscillation builds up.

Figures 5 and 6 show the distortion in the angular rotation. In Figure 5, the drive frequency is 11 Hz and the oscillation starts out at the driving frequency with corresponding EMG. Due to time-varying changes in the muscle's stiffness as the muscle contracts during each cycle, nonlinear behavior becomes progressively dominant with alternate stretch cycles becoming less prominent. The EMG pulses are also at half the driving frequency.

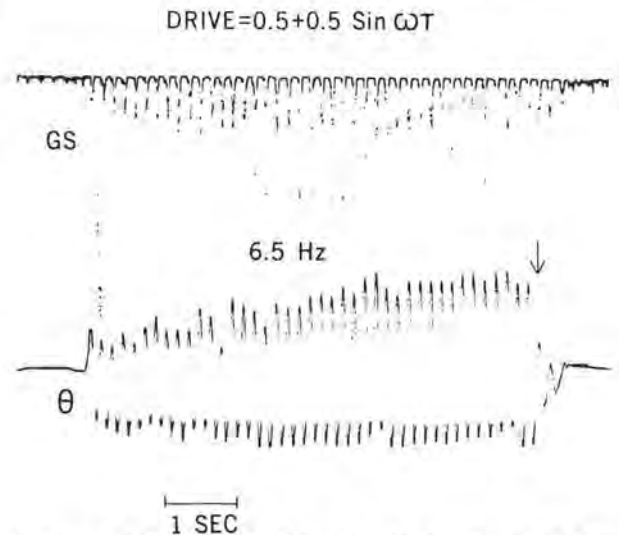


Figure 4. Slowly increasing amplitude of oscillation near the resonant frequency of 6.5 Hz. The upper trace is the EMG of the gastrocnemius-soleus muscle (rectified and filtered) and the lower trace is the angular rotation. The drive was $0.5 + 0.5 \sin \omega t$. The time markers are 1 second apart.

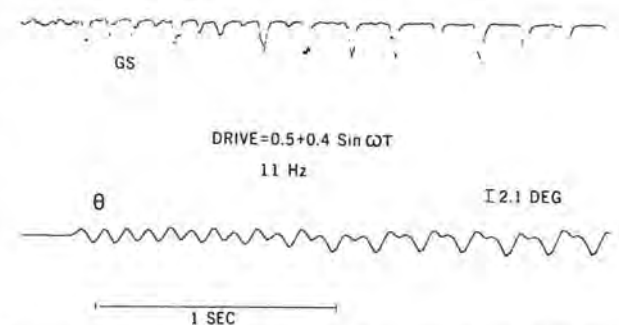


Figure 5. Forced oscillation of the ankle joint at 11 Hz. The upper trace shows the EMG activity of the gastrocnemius-soleus muscle (rectified and filtered) and the lower trace shows the angular rotation. The time markers are 1 second apart. For the first 1 second, the angular rotation is at 11 Hz and then gradually the nonlinear terms become prominent.

In Figure 6, the driving frequency is 10 Hz. The spontaneous recurrences of oscillation at the driving frequency (indicated by underlines) with corresponding 10 Hz frequency in the soleus EMG, are observed for a few cycles between periods of nonlinear oscillation.

Figure 6 also shows the autonomous oscillation of the foot after the modulating signal to the torque motor is turned off as indicated by the arrow. This free oscillation for the first 2 seconds after modulation is stopped is at 6.15 Hz as determined by Fourier transform analysis shown in Figure 7. Such self-sustained oscillations are always near the resonant frequency and not at the drive frequency. (The near-

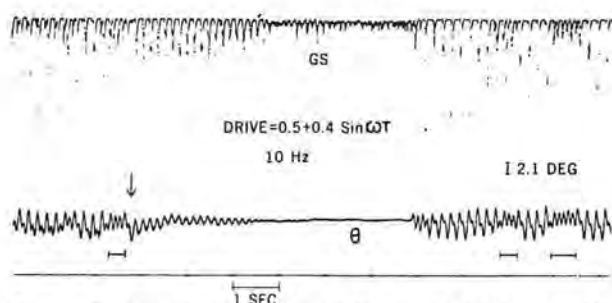


Figure 6. Forced oscillation of the ankle joint at 10 Hz. The upper trace shows the EMG activity of the gastrocnemius-soleus muscle (rectified and filtered) and the lower trace shows the angular rotation. The time markers are 1 second apart. The arrow indicates the time when the modulation signal of the motor was turned off. The self-sustaining oscillation of the ankle joint continued for several seconds near 6.15 Hz. As the modulation signal was turned on again, the nonlinear wave form rapidly developed. The recurrences of 10 Hz oscillations in between the nonlinear response are indicated by line segments underneath the angular rotation curve.

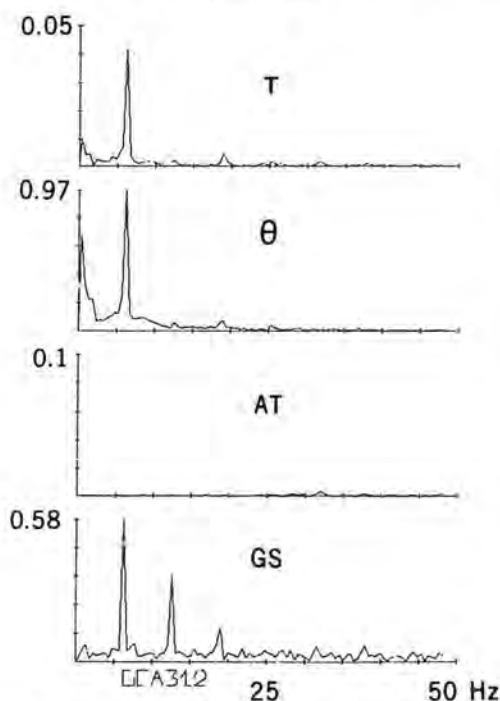


Figure 7. Fourier transform of the data for 2 seconds after the modulating motor signal was turned off as shown in Figure 6. The four traces from top to bottom are torque (Kg-meters), angular rotation (degrees), EMG of anterior tibial, and gastrocnemius-soleus muscles. The frequency of the self-sustaining oscillation was 6.15 Hz.

est drive frequencies tested were 5.5, 6, 6.25, and 6.5 Hz.) These oscillations are *not* voluntary in nature.

Figures 8 and 9 show the muscle compliance for six experiments when the amplitude of modulation was kept constant and the bias voltage changed from -0.5 to 0.75 volt. For the relaxed foot and zero motor bias voltage, the resonant frequency is at 4 Hz. For tonically active muscles, the resonant frequency is around 5.5 to 6.25 Hz.

Figure 10 shows the muscle compliance for the case when the bias is kept constant at 0.5 volt and the amplitude of modulation is varied with values of 0.2, 0.4, 0.5, and 0.6 volt. At 0.2 volt modulation, two peaks in the compliance curve are seen at 9 and 12 Hz; at 0.4 volt modulation, two peaks are seen at 6 and 6.5 Hz; at 0.5 volt modulation, one peak is seen at 6.25 Hz; and at 0.6 volt modulation, the two peaks are seen at 6.25 and 9 Hz.

Figure 11 shows the angular and torque power ratios defined as the ratio of power near the drive frequency divided by the total power of the signal. This ratio was obtained from the Fourier transform data by taking the sum of square of five frequency

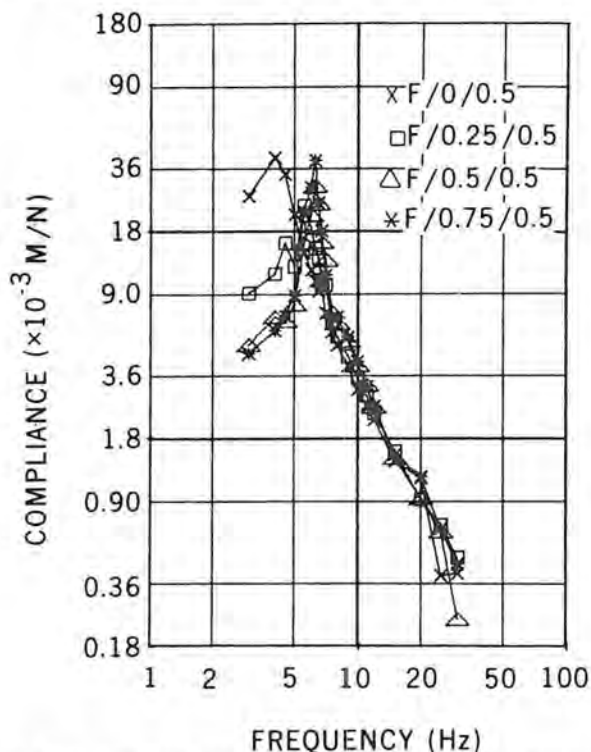


Figure 8. Effective compliance (angular rotation/torque Fourier coefficients) in meters/newton as a function of the input frequency. The amplitude of the modulation signal to the motor was kept constant at 0.5 volt. The motor bias voltages for the four cases were: x 0 volts, □ 0.25 volt, △ 0.5 volt, and * 0.75 volt. For positive nonzero motor bias the gastrocnemius-soleus muscle was tonically active to maintain the zero angular foot position. The resonant frequencies for these four cases were 4, 5.5, 6.25, and 6.75 Hz, respectively. (Subject GLG).

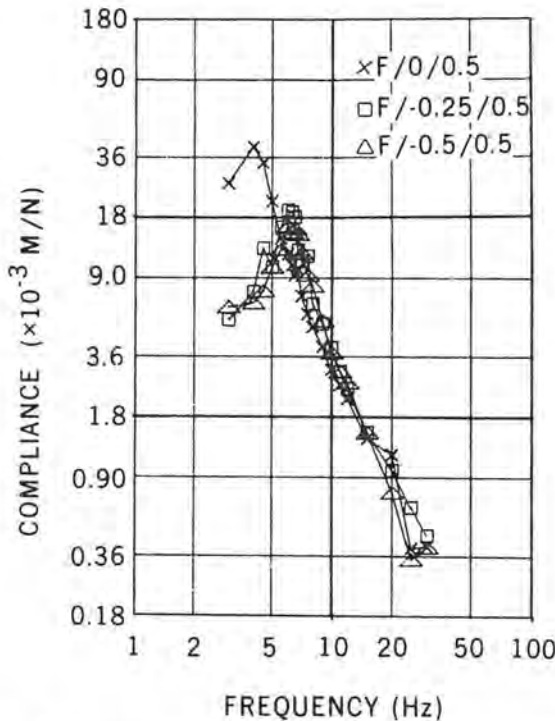


Figure 9. Effective compliance (angular rotation/torque Fourier coefficients) in meters/newton as a function of the input frequency. The amplitude of the modulation signal to the motor was kept constant at 0.5 volt. The motor bias voltages for the three cases were: \times 0 volts, \square -0.25 volts, and \triangle -0.5 volts. For negative nonzero bias the anterior tibial muscle was tonically active to maintain the zero angular foot position. The resonant frequencies for these three cases were 4, 6, and 6 Hz, respectively. (Subject GLG).

points nearest the drive frequency (± 1 Hz band) divided by the total sum of the squares, which represents the total power. In the range of 8 to 12 Hz, significant power of the angular rotation is in the subharmonics.

DISCUSSION

Figures 2, 3, 5, and 6 show the nonlinear nature of the system over the frequency range of 8 to 12 Hz. In the earlier studies by Joyce et al.¹⁴ and Walsh,^{17,18} these nonlinear effects were not observed because of their frequency sweeping technique. As illustrated in Figure 5, the nonlinear oscillation does not develop instantly, but the details of this behavior have not yet been fully investigated. The generation of subharmonics at these frequencies is most likely due to time-varying changes in the compliance of the rhythmically contracting muscle. The compliance of the human arm varies with contraction and, as calculated from Wilkie's data, is from 0.5×10^{-3} to 1.5×10^{-3} meters/newton.^{22,23}

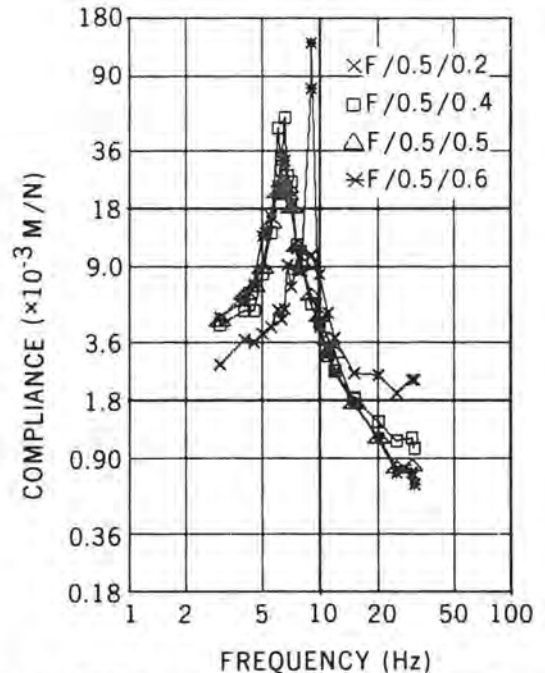


Figure 10. Effective compliance (angular rotation/torque Fourier coefficients) in meters/newton as a function of the drive frequency. The motor bias voltage was kept constant at 0.5 volt. The amplitude of the modulation signal for the four cases was: \times 0.2 volt, \square 0.4 volt, \triangle 0.5 volt, and $*$ 0.6 volt. The gastrocnemius-soleus muscle was tonically active against the motor bias to maintain the zero angular foot position. The resonant frequencies for these cases were: 6.75 and 8 Hz at 0.2 volt modulation, 6 and 6.5 Hz at 0.4 volt modulation, 6.25 Hz at 0.5 volt modulation, and 6.25 Hz and 9 Hz at 0.6 volt modulation. (Subject GCA).

Normal physiological tremor also has a frequency range of 8 to 12 Hz. Lippold²⁴ concluded that physiological tremor is due to oscillation in the stretch reflex servo-loop. One cannot exclude the possibility that the mechanisms responsible for physiological tremor interact with forced oscillatory inputs in this frequency range to produce these nonlinear modes of behavior.

The behavior of the system in Figure 6 is most interesting. The recurrences of 10 Hz oscillations in between the nonlinear response suggest that the system was near the boundary of linear and nonlinear regions. This behavior, coupled with the existence of self-sustaining oscillations that are emphasized with fatigue (in one experiment, a subject continued to oscillate for 58 seconds until he finally halted it), is surprising. The self-sustaining oscillations have been seen by Joyce et al.¹⁴ in the elbow movement. Such oscillations are due to the regenerative effects of the feedback loop and imply instability of the loop.

Conservative engineering design tends to emphasize stability, and this normally characterizes our view of

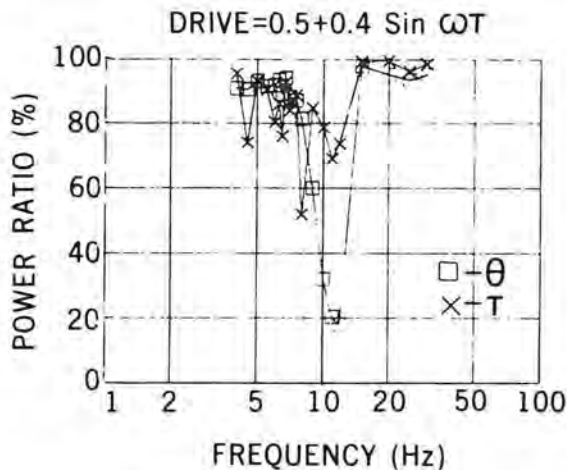


Figure 11. Angular rotation and torque power near the drive frequency as a function of the total signal power.

most physiological regulating mechanisms. An alternative view of many such regulators is that they are inherently unstable within some of their inner loops. Homeostasis is preserved, however, by the existence of outer loops that become active only near the boundaries of some allowable state space. Thus, the inherent instability is not observed except in cases of pathology or perhaps in experiments such as described here. Certainly none of our subjects have any history of neuromuscular illness nor have they any present complaints. None show ankle tremor and none have difficulty walking or driving, but all have experimentally demonstrated clonus. This is a most interesting paradox.

The slow buildup in the amplitude of oscillation near the resonant frequency (see Figure 4) is a common phenomenon in nonlinear systems. The "jump" phenomenon reported by Walsh¹⁸ near the resonant frequency of the wrist movement is commonly seen in mechanical systems with mass, damper, and a stiff spring. Such a system is described by Duffing's equation.²⁵

In Figures 8 and 9, the resonance of the relaxed foot is near 4 Hz. With tonic activity, the resonance is seen near 6 to 6.5 Hz. The resonant frequency is also dependent on the amplitude of modulation as seen in Figure 10. At 0.2 modulation, the resonance is seen near 8 Hz. At 0.4 and 0.5 modulation, the resonance is near 6.25 to 6.5 Hz. At higher modulation of 0.6, resonance is seen at 6.25 and 9 Hz. The second resonance, which is in the range of physiological tremor, very likely could be due to the stretch reflex mechanism.

These observations show the complexity of the peripheral stretch reflex system. Use of forced oscillations as the input to study these mechanisms provides an interesting avenue of investigation. Such investigations are of particular relevance to man-machine systems and job safety.

SUMMARY

1. Low frequency oscillations (3 to 30 Hz) were applied on the ankle joint in plantarflexion-dorsiflexion rotation using a torque motor. The torque and the angular rotation about the ankle and the evoked electromyograms from the gastrocnemius-soleus and the anterior tibial muscles were recorded.
2. Significant nonlinearities were observed in the angular rotation of the foot over the frequency range of 8 to 12 Hz with torque as the driving input.
3. Fourier coefficients at the drive frequency were used to calculate the effective compliance (angular rotation/torque), soleus EMG/rotation gain, and the phase relationship of torque—angular rotation and EMG—angular rotation. The compliance has sharp resonance near 6.5 Hz when tonic, voluntary muscle activity is present.
4. A two-cycle-averaged response was obtained for a 10-second data record by taking successive intervals equal to twice the modulation period. This shows significant nonlinearities in the angular rotation and the EMG over alternate cycles of stretch at the drive frequencies in the range of 8 to 12 Hz.
5. Fourier transform of a 10-second data record showed generation of harmonics and subharmonics of the drive frequencies. For the angular rotation, a significant proportion of the power is in harmonic frequencies when the drive frequency is from 8 to 12 Hz.
6. The following phenomena have been observed in the data: a) slowly increasing amplitudes of oscillation (to a limit) at drive frequencies near resonance; b) self-sustaining oscillations of the ankle joint near the resonant frequency after the modulation signal to the motor is turned off, particularly in the fatigued limb; and c) distortion (from the sinusoidal) of angular rotation during which there are spontaneous recurrences of oscillation at the drive frequency.

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QUESTIONS, ANSWERS, AND COMMENTARY

Question (D. Wasserman, NIOSH): We performed a similar study (unpublished, as a pilot study, and

not to the extent that you have performed it), Dr. Agarwal; we were concerned about the fact that the vibration exposure to the limbs of truck drivers, bus drivers, operators of heavy equipment, etc., was somewhat different than the vibration getting to the main trunk of the body because of the filtering characteristics of the seat in which they sat. Dr. Wright and I, acting as subjects, tried standing on a shaker. We programmed our shaker with the following conditions: 2.5 Hz (single sinusoidal), 5 Hz (single sinusoidal), and a final condition of a mixture of 2.5 Hz and 5 Hz, with each component having equal amplitudes and with zero phase between each component. Although our results are very inconclusive and it was very much a pilot study, we did notice that there was a period after the vibration ceased that the muscle continued to "fire" in a pattern analogous to when the vibration was present. We're terribly concerned from a worker safety point of view about how long that period lasts after the vibration has ceased. I wonder if you have any idea about how long that lasts, at least in your own work?

Answer: It is quite variable. For example in the work I mentioned, we applied vibration for 100 seconds continuously and when the motor was turned off, the oscillation continued for about 55 to 56 seconds. I was the subject; 10 minutes later I was still sitting there. We turned on the motor again for 100 seconds and turned off the motor. The second time it was only 15 seconds. The muscle was more fatigued now than the first time. So, it is quite variable. What causes this, we don't know. When we look at the motor physiology, we know very little at the levels of the higher brain centers, cerebral cortex, the mid-brain, and the cerebellum. The only thing that we have some knowledge about (and that, too, is not really precise) is at the spinal cord level mainly from animal experiments.

Question (D. Wasserman): Have you considered other muscles? Especially, the hand-arm system or supportive muscles such as the sacrospinalis?

Answer: The work done by Joyce et al. is at the elbow joint. Walsh is doing rotation of the wrist. The problem of rotation of the wrist that is you cannot perform a good EMG. We are building equipment to do the arm oscillation study where we can measure the biceps and triceps. But there, too, the difficulty is we are not just interested in the vibration and the EMG. We would like to superimpose the spinal reflexes. That's where we can get some information on what is happening at the spinal cord level. By just doing the peripheral measurement, there is no way you can tell what is happening at the spinal cord level. And that's where the limitations are for the elbow joint. But we will do the other studies. We are planning to do that.

Question (D. Wasserman): Have you at all examined spectral shifts in the myogram as a function of time under this stimulus?

Answer: Not systematically in terms of fatigue and

so on. There are quite a bit of data available, mostly controversial. No one has systematically done this. Actually, when you look at the shape of the Fourier transform of the EMG, what does this shape represent? In doing that, generally, you are doing surface electrode recording. From the neuron firing to the surface electrode recording, we have very little information.

What would be the effect, for example, when you talk about Henneman's principle as the muscle fatigues? You shift the motor units you are using. For different motor shapes, the motor unit potential is different. Thus, you can deduce that as the size of the motor unit changes, then that can cause a shift in the Fourier transform of the EMG. Systematically it has not been done by anyone to my knowledge.

Question (F. Dukes-Dobos, NIOSH): How did you establish the compliance of the muscle?

Answer: It was done simply. As I said, this is not really compliance of the muscle. Using the amplitudes in a Fourier series analysis of both the rotation and the torque, we took their ratio. Then, knowing the anatomy of the muscles (the radius of action is about 5 cm when you go to the back of the bone), you can convert that into what will be an effective value. What we are really measuring is torque, not force. If you can show that most of the torque was generated by the soleus muscle, you can tell what would be the effective force in the soleus muscle and what would be the effective stretch and simply take the ratio. But all this is not strictly in terms of compliance. First of all, the system appears to be nonlinear. Secondly, to define a compliance as a number is wrong because we do know the compliance of the muscle changes with muscle activation. As the muscle goes through different phases of the cycle, the compliance is a function of time. Whether we can get that at all by this kind of analysis I have described, I would say is impossible.

Question (H. Von Gierke, Aerospace Medical Research Laboratory): We had done studies in our laboratory, too. Using human subjects, Dr. Coormann started in the fifties on the so-called suppression of reflexes under vibration. After several years we gave it up. It was leg vibration only, not whole-body vibration. Dr. Hague in our laboratory studied the cat and I'm not fully prepared to recall the results of his studies, but they are published. He studied the gastrocnemius of the cat, attaching the muscle to a kind of leg puller. He applied the vibration directly as a stretch stimulus to the tendon and then superimposed on this, individual stimuli to excite the tendon. If I recall correctly, one of his main results was that the so-called suppression is really more a masking phenomenon. In these experiments, he increased the vibration level successively and left the stimulus constant until the vibration interfered with the stimulus; therefore, there was no individual reaction to the so-called stimulus anymore. He more or less explained this by a kind of model, and I think he finally came to the conclusion that his model was not very good

because it did not consider the antagonistic action of the two muscles. He then was sidetracked and showed that the nonlinearity you have in one muscle is really compensated in the complete system by the antagonistic muscle and that the action of the two muscles really gives you a fairly linear system, so to speak, in push-pull operation.

Answer: I'm not familiar with that particular research, but the best work I've seen done in this area came from Australia and Arizona. Lance has done quite a bit of work in that particular area, too. I don't know if you're familiar with his work. There are problems with this work. First of all you cannot isolate the antagonist muscle. When working with a cat, generally removal of the antagonist muscle is easily accomplished. Removal of the antagonist muscle allows one to see whether that muscle had any contribution to the muscular action under study. For example, take the muscle tendon, attach it to the puller (which is basically some kind of vibrator) like a speaker system which goes back and forth; if you want a tonic reflex in that muscle (a so-called "tonic stretch reflex"), in effect you modulate the normal muscle input with a vibrating signal. This represents a stretch input. But actually, the input to the system is not the stretch due to vibration; the input to the system is the resultant stretch of the spindle, and there is no way to measure that—there's no way to control it. The Hoffmann reflex gives you a slightly better result, then, because you are working on the nerve rather than relying on the spindle. So with the tendon jerk one will have problems.

Question (H. Von Gierke): But you still have a bigger problem with your rotation, because with increasing frequency your stretch will be concentrated more at the higher frequencies than at the lower frequencies.

Answer: I agree with you. You cannot do the rotation type of experiment when you are talking about 50 Hz, 100 Hz and so on. Most of the work done on cats has either been at 50 Hz or 100 Hz. Some work at Homma's lab lately has come out at 150 to 200 Hz, as well. The rotation we are talking about at 8 to 12 Hz is where we see the physiological tremor. So the system is quite capable of oscillation in that particular range. At the moment, we have no way of saying what the physiological tremor has to do with the forced oscillation, and how they interact. One of the experiments that we would ultimately like to do (and I don't know whether we would have permission to do that in the hospital where we are working) is to block the nerves. Here, too, there are uncertainties. What exactly have you blocked when you apply Procan? Have you blocked the Gamma system and at what point have you started blocking the motor system, etc?

In terms of the human physiology, we barely know anything. In terms of the cat, we have opened it up and all we know are the physiological interconnections. Beyond that, I doubt if any physiologist can say anything about how the motor system works.

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