Tonic and phasic spinal cord mechanisms in man

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Skilled movements of any sort require the assumption of an appropriate posture. Most skilled movements comprise rapid, repetitive, alternating and coordinated activity, chiefly of distal muscles. Most postures demand constant sustained activity chiefly of proximal muscles and flexor groups in the upper limb and extensor groups in the lower limb. These functions of voluntary movement, designated respectively as phasic and tonic, have their counterparts in reflex action. The tendon jerk (or its reflex equivalent elicited by electrical stimulation of afferent fibres) results from a neural discharge so brief as to be classified as a phasic response, while the maintained reflex contraction elicited by more prolonged muscle stretch in a suitably tense subject or a spastic patient has the duration of a tonic response.

It is of considerable interest to know whether there are two different populations of alpha motor neurones in the anterior horns of the spinal cord, each with separate characteristics, and which innervating a particular type of muscle fibre, or whether a particular cell might alter its properties depending upon the manner of its activation and the prevailing influence of other cells upon it. By recording from single efferent fibres of the ventral nerve roots of decerebrate cats, Granit, Henatsch, and Steg (1956) were able to divide motor neurone responses fairly clearly into two categories. Motor neurones, which discharged once or twice on the rising phase of the stretch stimulus, did not continue to discharge during sustained stretch, and were not affected by a preceding afferent tetanus, were classified as phasic (53 out of 100 motor fibres studied). Motor neurones whose activity continued during the plateau of stretch and was greatly increased by preliminary tetanization were classified as tonic (found in 44 out of 100 fibres). Three fibres fired continuously during sustained stretch with or without a conditioning afferent tetanus. It was noted that small spike potentials were usually those of tonic cells and the larger potentials were associated with phasic responses. Granit, Phillips, Skoglund, and Steg (1957) reported that repeated brief muscle stretches, twisting the pinna of the ear and tetanic stimulation of the contralateral sural nerve (crossed extensor response) all potentiated tonic motor neurone activity without altering phasic activity, in a manner similar to monosynaptic tetanic stimulation. These authors commented that deterioration in the state of the animal or deep anaesthesia immediately abolished tonic responses, whereas phasic reflexes were much more resistant.

They conclude that there are two systems of ventral horn cells for extensor muscles in the cat, the small tonic cells being capable of building up facilitatory states of long duration by means of polysynaptic connexions (tonic interneurones) as well as monosynaptic connexions. All tonic cells are inhibited by antidromic stimulation (recurrent or Renshaw cell inhibition) while some phasic cells are unaffected and the tendon jerk persists unaltered (Granit, Pascoe, and Steg, 1957).

It is apparent from clinical observation that tonic and phasic mechanisms may be affected differentially in man. A patient with cerebellar disease is commonly ‘hypotonic’ in the sense that the limbs may be moved freely at a joint without any active muscular resistance being sensed by the examiner, and yet the tendon jerks are usually brisk, a combination which gives rise to the undamped or pendular knee jerk. The converse situation with rigid or spastic limbs but diminished tendon reflexes is also seen but has been explained as occlusion of phasic reflexes by tonic reflexes engaging all available cells of the motor neurone pool (Denny-Brown, 1929). Tonic stretch reflexes are increased in Parkinson’s disease without any consistent change in phasic reflexes. How does this divergence in the intensity between tonic and phasic stretch reflexes come about when, as far as is known, both share the same monosynaptic reflex pathway? In man, are there separate populations of tonic and phasic anterior horn cells which react differently to afferent stimulation as have been demonstrated in the cat? Or is there only one type of alpha cell which discharges once in response to a synchronous

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afferent volley but fires repetitively when subjected to a sustained asynchronous barrage?

Recently it has been shown that continued vibration of muscle in man produces differential effects on tonic and phasic reflexes. The muscle spindle is well known to be sensitive to vibration from the work of Echlin and Fessard (1938), Granit and Henatsch (1956), and Bianconi and Van der Meulen (1963) and this sensitivity is increased by stimulation of both types of fusimotor fibre (Crowe and Matthews, 1964). A brief vibration of muscle, such as that set up by percussion of the muscle belly or tendon, or by tapping a bony prominence in more remote parts of the limb, will induce a phasic reflex contraction of muscle since the propagated vibration wave applies a brief stretch stimulus to intrafusal fibres (Lance and de Gail, 1965). On the other hand, the continued application of a vibrating object to the muscle belly progressively suppresses phasic reflexes while at the same time contraction slowly develops in the muscle vibrated. There is evidence that these phenomena result from stimulation of the muscle spindle by vibration, initiating activity in group Ia afferent fibres (Lance, 1965; de Gail, Lance, and Neilson, 1966). Hagbarth and Eklund (1965) have reported that vibration of muscle tendon in man will produce a tonic contraction of the muscle concerned, and Matthews (1966) has confirmed the presence of this phenomenon in the decerebrate cat.

To explain the differential effect of vibration on tonic and phasic spinal mechanisms, de Gail et al. (1966) found it necessary to postulate the presence of both tonic and phasic anterior horn cells in man. This concept has been re-examined in the light of further evidence presented in this paper as a result of physiological, pharmacological, and clinical studies.

PROCEDURE

The methods employed were standard for elicitation of the H reflex and tendon jerks, using a surface lead electromyogram (E.M.G.) and recording the force of isometric muscle contraction by a strain gauge applied to the appropriate part of a limb. Angular displacement of a limb during isotonic contraction was measured by a potentiometer attached to a lever which was strapped to the limb. A Disa bipolar electrode was used for the intramuscular recording of single motor units. The responses were displayed on a Grass polygraph, a Tektronix storage oscilloscope, or both. Orbital vibrators were applied to muscle belly or tendon, usually at a frequency of approximately 50 c.p.s. Further details will be found in the paper of de Gail et al. (1966).

RESULTS

Tonic contraction commonly starts a few seconds after the application of a vibrator to muscle belly or tendon even if the muscle is previously relaxed, but on occasion there may be a variable latency in this period. Some muscles, such as the biceps brachii, require to be in a state of partial contraction (sufficient to keep the forearm elevated against gravity) for the phenomenon to be elicited. The tonic contraction increases progressively until a plateau is reached after about 30 seconds. Immediately after removal of the vibrator from the muscle belly, the tonic contraction starts to diminish but E.M.G. activity may be recorded from the muscle for up to a second during the period of relaxation (Fig. 1). This tonic contraction may be inhibited voluntarily but recurs if the subject's mind is distracted.

REINFORCEMENT The height of tonic contraction in the quadriceps is not substantially affected by clenching the fist or pulling one hand against the other (Jendrassik manoeuvre), although the suppression of tendon jerks by vibration is partially overcome by such methods of reinforcement. When the ear of a human subject is twisted firmly (causing moderate pain) while a tonic contraction is being elicited, an augmentation of the force of contraction is usually observed and ceases when the stimulus is withdrawn. This 'pinna reflex' effect may be repeated a number of times.

EFFECT OF MUSCLE STRETCH When a tonic contraction of the quadriceps reached its maximum in a sitting subject with the leg unrestrained, the lower limb assumed a position between 30 and 45 degrees short of full extension. The muscle was then subjected to slow stretch by flexing the knee while the
tonic contraction continued, giving the clinical impression of plastic rigidity to the examiner. If the limb were flexed rapidly, the tonic contraction was abolished clinically and electromyographically but soon developed again. When the limb was flexed and extended with a rapid sinusoidal motion, the tonic reflex was recorded while the limb was in a relatively extended position but disappeared when the limb was relatively flexed. It therefore appeared that the response was temporarily abolished by a critical degree of muscle stretch.

**INHIBITION BY VIBRATION OF ANTAGONIST** While the quadriceps was being vibrated and tonic contraction was in progress, a second vibrator was applied to the tendons of its antagonist, the hamstrings muscles. When the second vibrator was switched on, the quadriceps contraction ceased after a short latent period, even though quadriceps vibration continued (Fig. 2). When the second vibrator was switched off, the quadriceps contraction recurred. On some occasions a limited quadriceps contraction recurred even while vibration was being applied to the hamstrings, but it reverted to its full force only when the hamstrings vibration stopped. The converse was also demonstrated in that a vibration-induced contraction of hamstrings was abolished by vibrating the quadriceps or its tendon, thus illustrating that the principle of reciprocal innervation applies to vibration-induced tonic contraction. Surface-lead electromyography of hamstrings and quadriceps demonstrated that tonic contraction was inhibited by vibration of the tendons of the antagonist before any tonic contraction had been induced in the antagonistic muscles (Fig. 3).

**POST-TETANIC POTENTIATION OF THE H REFLEX AND TONIC CONTRACTION** In our hands, post-tetanic potentiation of the H reflex, a phasic reflex, has been extremely variable in individual subjects, and from subject to subject. We have used tetani of 20, 50, 100, 300, and 500 per second, applied to the posterior tibial nerve for periods of 5 and 10 seconds. The procedure has been repeated with test H reflexes varying from 10% to 70% of the maximal H reflex, with conditioning tetani of the same voltage as well as with conditioning tetani of a voltage sufficient to elicit a maximal H reflex when applied as a single shock. Test shocks have been administered repetitively once every five seconds after cessation of the tetanus as a routine but on other occasions single test shocks have been applied at variable intervals after tetanus. At least one minute was allowed to elapse between successive sequences. Post-tetanic potentiation of H reflexes was not obtained consistently with any combination of conditioning or test shock. The results can be summarized as follows:— Tetani of 20 c.p.s. always produced post-tetanic depression. Tetani of 50 c.p.s. either depressed or left unaltered the test response. Tetani of 100, 300, or 500 c.p.s. sometimes produced striking post-tetanic potentiation (so that the test H reflex approximated its maximal value) lasting for some minutes. On other occasions, with no obvious alteration in the technique of stimulating and recording, little or no potentiation was obtained. The factors which appeared to favour the appearance of post-tetanic potentiation were (a) frequency of
conditioning tetanus of 100 c.p.s. or more; (b) higher voltage being used for conditioning tetanus than that required for test shock; (c) lower voltage of test shock, i.e., test H reflex well submaximal; (d) pain induced by tetanic stimulation.

The phenomenon of post-tetanic potentiation was also exhibited by vibration-induced tonic contraction of the gastrocnemius-soleus muscle in four out of five normal subjects, being consistently obtained in two subjects. When the tonic contraction had reached its plateau, a tetanus of 500/sec. for 10 seconds was applied to one posterior tibial nerve. Tonic contraction ceased for some seconds after the tetanic contraction finished, but then recurred with increased force (Fig. 4). Figure 5 shows a graph of post-tetanic potentiation of tonic contraction contrasted with post-tetanic potentiation of H reflexes on the same day in the same normal subject.

**DISCHARGE FREQUENCY OF SINGLE MOTOR UNITS DURING VIBRATION-INDUCED TONIC CONTRACTION**

A Grass accelerometer was strapped on the part of the limb to be vibrated, and a Disa bipolar electrode inserted through the gastrocnemius into the soleus muscle. When tonic contraction was established by vibrating the tendon of the muscle concerned, the frequency of vibration was increased in steps from 30 to 80 c.p.s. While vibration frequency and the discharge of single motor units was recorded on the oscilloscope and photographed. The rate of firing of single units varied from 4 to 10/sec. irrespective of the frequency of vibration. Increasing the frequency of vibration brought into play more units, thus increasing the force of tonic contraction but did not increase the discharge rate of individual units in the soleus beyond 10/sec.

**EFFECT OF DRUGS ON TONIC CONTRACTION**

It has already been shown that the injection of thiopentone and the triazine compound Ciba 28,882 Ba (Bein and Fehr, 1962) abolishes vibration-induced tonic contraction simultaneously with the abdominal reflexes, while tendon jerks are preserved (de Gail et al., 1966). Diazepam (Valium) was found to have a similar effect. Intravenous administration of 10 mg. diazepam temporarily abolished tonic contraction together with the abdominal reflexes in three normal subjects and recovery took place over 35 to 80 minutes (Fig. 6). A sensation of relaxation and slight drowsiness was experienced by the subjects.

Benztropine methanesulphonate (Cogentin), 2 mg., was injected intravenously into the same three normal subjects when vibration-induced tonic contraction had reached a plateau. The contraction was suppressed slowly over a period of five to seven minutes, to return gradually and incompletely over the hour it was observed (Fig. 7). Unlike the action of the drugs previously mentioned, abdominal reflexes were not abolished by benztropine. It is noteworthy that tendon jerks (and the suppression of tendon jerks during vibration) were not altered, even at the height of action of these drugs.

Intravenous sodium phenytoin (Dilantin) and
edrophonium (Tensilon) did not affect the tonic contraction.

**CLINICAL ASPECTS OF TONIC CONTRACTION** Four patients with unilateral nerve root lesions did not exhibit a tonic contraction in the muscle whose tendon jerk was absent, while the tonic contraction was normal on the unaffected side. Two patients with partial reduction of tendon jerks showed a comparable reduction in tonic contraction on the affected side (Table I). Muscle power and sensation were normal to clinical examination in all six patients.

No tonic contraction could be elicited in four patients with peripheral neuritis but one patient with peroneal muscular atrophy (Charcot-Marie-Tooth disease) in whom there was a stocking loss of sensation, did show a tonic contraction in the quadriceps although the knee jerk was clinically absent.

In patients with chronic cord transection in the lower cervical or upper thoracic region, tonic contraction was normal in muscles innervated from segments above the site of the lesion but was absent below the lesion in 11 out of the 12 patients. In the twelfth patient, the contraction was inconstant and feeble.

The tonic reaction was reduced in seven patients with cerebellar disorders, more markedly on the side of greater deficit. It was absent on the affected side of one patient with a unilateral cerebellar syndrome caused by haemorrhage from a cerebellar angioma. In a boy of 17 with Friedreich's ataxia no tonic contraction could be induced in the lower limbs where deep reflexes were absent, but in the

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**TABLE I**

**THE EFFECT OF CLINICAL LESIONS UPON VIBRATION-INDUCED TONIC CONTRACTION**

<table>
<thead>
<tr>
<th>Site and Type of Lesion</th>
<th>No. of Patients</th>
<th>Tendon Jerks</th>
<th>Tonic Contraction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nerve root compression (unilateral)</td>
<td>4</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Peripheral neuritis</td>
<td>2</td>
<td>Reduced</td>
<td>Reduced</td>
</tr>
<tr>
<td>Rostral cord transection</td>
<td>5</td>
<td>Absent</td>
<td>Four absent, one present</td>
</tr>
<tr>
<td>Cerebellar deficit</td>
<td>12</td>
<td>Increased</td>
<td>Eleven absent, one reduced</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Present</td>
<td>Five reduced or absent on more affected side, two reduced or absent bilaterally</td>
</tr>
<tr>
<td>Midbrain thrombosis</td>
<td>1</td>
<td>Present</td>
<td>Present (induced 'red nucleus tremor')</td>
</tr>
<tr>
<td>Friedrich's ataxia</td>
<td>1</td>
<td>Present (upper limbs)</td>
<td>Reduced on side of greater cerebellar deficit</td>
</tr>
<tr>
<td>Upper motor neurone lesions (a) Cerebral</td>
<td></td>
<td></td>
<td>Absent in lower limbs</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Six reduced on affected side, two on both</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Absent in affected arm and both legs</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reduced below lesion bilaterally</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Normal</td>
</tr>
<tr>
<td>Parkinson's disease</td>
<td>8</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Dystonia</td>
<td>2</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Anoxic decerebrate rigidity</td>
<td>1</td>
<td>Increased</td>
<td>Absent</td>
</tr>
</tbody>
</table>

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**FIG. 6.** Effect of diazepam. Force of tonic contraction induced by vibration of quadriceps muscle measured before, and at intervals after, intravenous injection of diazepam 10 mg. Results shown for three normal subjects. Tonic contraction is rapidly abolished, but returns after half to one and a half hours. Abdominal reflexes were also abolished.

**FIG. 7.** Effect of benztropine methanesulphonate. Force of tonic contraction induced by vibration of quadriceps muscle measured before, and at intervals after, intravenous injection of benztropine methanesulphonate 2 mg. Results shown for three normal subjects. Tonic contraction is rapidly abolished, the suppression being prolonged. Abdominal reflexes persisted throughout.
upper limbs tendon jerks and tonic contraction were present, the latter being reduced on the side of greater cerebellar disturbance.

One patient had suffered from the onset of a coarse postural tremor of the left arm and leg at the same time as a right third nerve palsy as the result of mid-brain thrombosis. She was completely free of tremor at rest. Application of a vibrator to the left biceps initiated a tonic contraction, and with it her characteristic postural tremor.

Nineteen patients with upper motor neurone lesions have now been studied, apart from the 12 patients with spinal transection mentioned above. Tonic contraction was diminished in all patients except one with a diffuse brain-stem lesion in whom it was absent. When there was asymmetry of tendon jerks, the tonic contraction was less forceful on the side of hyper-reflexia, although in two out of eight patients with hemiparesis of cerebral origin tonic contraction was diminished but symmetrical. Vibration induced a normal contraction in eight patients with Parkinson’s disease but not in two patients with dystonia (one with dystonia musculorum deformans and one with a dystonia secondary to progressive post-encephalitic athetosis). The reaction was absent in one patient with post-anoxic decerebrate rigidity.

CLINICAL ASPECTS OF PHASIC REFLEX SUPPRESSION BY VIBRATION Muscle vibration greatly diminished or abolished the phasic deep reflex (tendon jerk or H reflex) of the appropriate muscle in all patients with normal reflexes. The effect was less pronounced in patients with the hyperreflexia of upper motor neurone lesions, and in some patients with very brisk reflexes, the degree of suppression was barely perceptible. In the patient with Friedrich’s ataxia a small H reflex could be elicited in spite of the absence of ankle jerks, and was not suppressed by vibration of the triceps surae. Since muscle spindles are known to degenerate early in Friedrich’s ataxia (Mott, 1907), this supports the view that the normal suppressive effect of vibration depends upon the spindle.

SINGLE UNIT RECORDING IN TONIC AND PHASIC REFLEXES The apparent paradox of phasic reflexes being suppressed while a tonic reflex was elicited suggested the possibility of two different types of motor neurone which were affected differentially by the reflex effects of vibration. It therefore became of importance to determine whether a given motor unit played a part in both tonic and phasic reactions. In three normal subjects a Disa bipolar electrode was inserted deeply into the medial and proximal part of the calf so as to pass through the gastrocnemius into the soleus near its origin. An H reflex was produced by stimulation of the posterior tibial nerve and the electrode position altered until a single motor unit was recorded and photographed. A tonic contraction was then initiated by vibration of the tendo Achillis and the resulting unit discharge photographed. This process was repeated until a single unit was found which discharged consistently with both tonic contraction and H reflex. The procedure was time consuming since the muscle

FIG. 8. Single motor unit participation in tonic and phasic reflexes.
A An E.M.G. recorded from gastrocnemius-soleus, through surface electrodes, following single shock to posterior tibial nerve. Stimulus strength chosen to elicit H reflex without apparent (M) response. Artefact on left.
B An E.M.G. recorded simultaneously through Disa bipolar needle electrode, showing participation of single motor unit in H reflex.
C Three random samples (50 msec. duration) recorded from needle electrode during tonic contraction of gastrocnemius-soleus induced by vibration of tendo Achillis. One motor unit is recorded, and this has the same appearance as the unit recorded during H reflex elicitation.
D Two random samples (50 msec. duration) recorded from needle electrode during slight voluntary contraction of gastrocnemius-soleus, i.e., plantar-flexion. The same motor unit is again recorded.
shortening produced by phasic or tonic contraction shifted the electrode position slightly so that a single unit discharge was frequently lost or altered in appearance in the transition from one form of stimulation to another. Figure 8 illustrates a single unit which discharged consistently as part of the H reflex as well as with vibration-induced tonic contraction and sustained voluntary contraction.

**DISCUSSION**

It has been shown that a given motor unit may participate in both tonic and phasic reflexes. Is there any way in which phasic reflexes may be occluded by the effects of vibration and still permit a tonic contraction to develop? The suppression of phasic reflexes cannot be explained solely by the vibratory stimulus engaging the muscle spindle receptors and making them unresponsive to tendon tap, because H reflexes, which do not depend directly upon the spindle, are also suppressed. However, Hunt (1952) demonstrated that steadily increasing the amount of muscle stretch reduced the size of the monosynaptic response progressively in spinal cats. He attributed this to central effects of the afferent discharge evoked by steady stretch. Recently Henneman (personal communication) has shown that the electrical excitability of group I afferent fibres is diminished by stretch of their muscle of origin, even when these fibres are sectioned central to the recording site, i.e., that sufficient afferent activity is generated by stimulation of spindle endorgans to produce a 'busy line'. This would account for diminution of the monosynaptic reflex in the intact animal, without the necessity for postulating a central inhibitory effect. It is probable that the same mechanism is operating in our experiments since sustained vibration of muscle would be expected to produce continuous afferent activity in the same manner as steady stretch, thus suppressing tendon jerks and H reflexes by reducing the number of afferent fibres available for stimulation. If this be the case, two problems remain.

1. The five-second period required for recovery of H reflexes after vibration ceases (de Gail et al., 1966): this prolonged depression of excitability is much the same after a single conditioning H reflex or after repetitive afferent stimulation, and probably depends upon a central mechanism.

2. The reversibility of tendon jerk suppression by reinforcement and the relative ineffectiveness of vibration in reducing the hyperactive reflexes of a spastic patient.

It is now considered that reinforcement increases excitability of alpha cells as well as gamma, since the H reflex, which bypasses the spindle mechanism, may be reinforced (Landau and Clare, 1964a). The same authors (1964b) have also shown that the H reflex is augmented on the affected side of hemiplegic patients, indicating a state of facilitation of alpha cells. Under these circumstances, the synchronous burst of afferent activity produced by tendon tap or posterior tibial nerve stimulation may produce an increment of activity above the asynchronous afferent discharges of the 'busy line' produced by vibration, which is sufficient to produce a significant reflex discharge of the facilitated alpha cells.

The studies of experimental tonic contraction presented here indicate that it depends upon vibration stimulating muscle spindle receptors to produce impulses in group Ia afferent fibres. Because muscle spindles are scattered throughout muscle bellies, each having an afferent path to the spinal cord of different length, and because the vibration wave propagates irregularly through muscle, it is probable that vibration-induced afferent activity is asynchronous by the time it arrives at the alpha anterior horn cell. In spinal man, although the alpha cell is known to be in a state of facilitation for the passage of phasic reflexes, the asynchronous vibration-induced afferent activity does not usually induce a tonic contraction. This is surprising, since the presence of post-tetanic potentiation indicates that vibration-induced tonic contraction has a monosynaptic component, although it is dependent upon supraspinal centres for its full development.

Post-tetanic potentiation of the H reflex, a phasic reflex which is monosynaptic under normal circumstances, has been demonstrated by Hagbarth (1962) and Corrie and Hardin (1964). We found the degree of post-tetanic potentiation of H reflexes and even the presence or absence of the phenomenon to be unpredictable in any one subject under carefully standardized experimental conditions. The situation in intact man is much more complex than that of the experimental animal. Granit (1956) has shown that post-tetanic potentiation is much shorter in duration when the nerve to gastrocnemius-soleus is intact than when it is severed, even in a decerebrate cat with a de-efferented hindlimb! Post-tetanic potentiation of tonic reflex contraction could be demonstrated in normal subjects in the majority of instances. Following the tetanus, the contraction ceased for a short period, which may be related to blockade of muscle spindle function by antidromic impulses in the afferent nerves stimulated (Granit et al., 1956). After the phase of post-tetanic potentiation, the tonic contraction frequently underwent a period of depression before recovering to normal levels.

The supraspinal structures which appear to be
essential for the augmenting nature of vibration-induced tonic contraction are the cerebellum and the upper motor neurone. It is postulated that the extensive group Ia afferent projection to the cerebellum may reflexly reinforce spinal mechanisms through the upper motor neurone, since stimulation of deep cerebellar nuclei is known to influence gamma and alpha neurones (Henatsch, Manni, Wilson, and Dow, 1964; Henatsch, Manni, and Dow, 1964). It is known that gamma activation increases the sensitivity of the spindle to vibration (Granit and Henatsch, 1956). Matthews (1966) has recently demonstrated that vibration of the soleus tendon in the cat evoked a tonic contraction of the muscle belly which was undoubtedly reflex, for it was abolished by cutting the muscle nerve and inhibited by stimulating the central end of the cut peroneal nerve. It was present in the decerebrate animal and persisted after ablation of most of the cerebellum. It was abolished by high cervical spinal section and by an anaesthetic dose of pentobarbitone. The phenomenon appears to be identical to that which we have described and its persistence in the cat after removal of the cerebellum is the only serious discrepancy between the findings in cat and man.

Various drugs used in this study abolished tonic contraction without affecting phasic responses. This could be explained by polysynaptic blocking action with the exception of benztrpine methanesulphonate (Cogentin) which did not reduce the abdominal reflexes. All these drugs may impair the ability of the anterior horn cell to respond to asynchronous afferent stimuli, i.e., decrease its susceptibility to temporal summation in a non-specific manner like anaesthesia. Alvord and Fuortes (1953) remarked that 'anaesthetized preparations, though giving reflex reactions to single shocks . . . , do not respond to stimuli other than sudden and can only react with unsustained activity. Apparently they lack the properties which normally allow reactions to gradual stimuli and secure sustained reflexes.' Alvord and Fuortes went on to show that in decerebrate cats there was no relation between the frequency of afferent activity recorded from the dorsal nerve roots in response to stretch and the regular frequency of reflex unitary motor discharge at about 10/sec. Long latencies were found between start of repetitive stimulation and initiation of the tonic reflex discharge. Alvord and Fuortes postulated that asynchronous afferent discharges from muscle built up a central excitatory state which was necessary for the generation of sustained reflexes.

The vibration-induced tonic contraction in man has characteristics different from those of spasticity or extrapyramidal rigidity. It is more variable in latency and intensity than the abnormal tonic stretch reflexes found in these conditions and is abolished rather than augmented by the application of sudden stretch to the muscle. Vibration-induced tonic contraction is a physiological reaction found in its most complete form in normal subjects and may be considered as a means of testing the pathway for tonic stretch reflexes in intact man. The fact that this reaction is diminished in patients with upper motor neurone lesions, who show the increased tonic stretch reflexes of spasticity, implies that the latter are not simply exaggerated normal responses, but employ only part of the normal pathway, being deprived of the supraspinal connections required for the normal graded augmenting reflex contraction.

Considering the present evidence, there does not appear to be any need to postulate separate tonic and phasic anterior horn cells in man. The anterior horn cell pool may react phasically if it is presented with a synchronous afferent volley when in an adequate state of excitation. Under normal circumstances when the afferent barrage is asynchronous, from muscle stretch or an artificial stimulus such as vibration, the anterior horn cell pool has to be raised progressively to a higher state of excitation in order to respond with sustained tonic discharge. The manner in which this process depends upon supraspinal structures in intact man remains uncertain.

Evarts (1965) has recently shown, in recordings from the unanaesthetized monkey, that pyramidal neurones of high axonal conduction velocities are active mainly during movement while those of low conduction velocity tend to discharge tonically. This supports the suggestion made by Brookhart (1952) that small pyramidal fibres may be more concerned with tonic functions and the larger fibres with phasic movement. Two fibre groups of different conduction velocity were demonstrated in the cat. Pyramid by Bishop, Jeremy, and Lance (1953). They both arise from the same areas of somatosensory cortex (Lance and Manning, 1954) and can both be traced down to the lumbar segments of the cord (Lance, 1954). The presence of two fibre groups in the pyramid was confirmed by Patton and Amassian (1960), their origin from the cortex by Towe, Patton, and Kennedy (1963), and their presence in subcortical white matter by Takahashi (1965). It is of interest that Szentagothai-Schimert (1942) found two modes of distribution of fibre diameter at 1 μ and 7 μ in the human pyramid. In view of Evart's findings, the smaller group of pyramidal fibres may well serve the function of maintaining a suitable background excitability of alpha spinal cells so that they become responsive
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to the temporal summation of asynchronous stimuli and thereby capable of mediating physiological tonic reflexes.

Tonic stretch reflexes are of greater physiological and clinical significance than phasic stretch reflexes. They comprise the 'muscle tone' of the clinician and determine posture. It remains to be seen whether vibration-induced reflex contraction will serve as a means of testing tonic mechanisms in a manner comparable with the tendon jerk for phasic mechanisms.

SUMMARY

Sustained vibration of muscle in normal man suppresses phasic reflexes (tendon jerks, H reflexes) and provokes a reflex tonic contraction in the muscle vibrated. This tonic contraction is abolished by simultaneous vibration of the muscle antagonist and can be potentiated by a conditioning tetanus applied to the muscle nerve. The evidence suggests that vibration stimulates the muscle spindle, thus producing activity in group Ia afferent fibres, and the presence of post-tetanic potentiation implies that tonic contraction is mediated at least in part through the monosynaptic reflex arc. The fact that the reaction is diminished in lesions of the cerebellum or upper motor neurone indicates that it is dependent upon connexions with supraspinal structures in contrast to the abnormal tonic reflexes found in spasticity. The force of tonic contraction increases as the frequency of vibration is increased up to about 80/sec, but single motor units continue to discharge at 6 to 10/sec.

The diminution of phasic reflexes by vibration is best explained by most of the group Ia afferent fibres being occupied with the asynchronous activity produced by vibration, so that only a small increment of activity can be produced by a synchronous volley. This explanation for occlusion of phasic responses in the peripheral nerve obviates the necessity for postulating two separate groups of tonic and phasic motor neurones affected differentially by vibration. This is supported by the demonstration of the same single motor unit participating in voluntary contraction, vibration-induced tonic contraction, and the H reflex.

Vibration-induced tonic contraction was diminished or abolished by thiopentone, Ciba 28,882 Ba, diazepam and benztropine methanesulphonate. It was unaltered by phentoyin and edrophonium.

Tonic contraction was diminished or absent in lesions of the appropriate nerve root or in patients with peripheral neuritis. It was absent in the majority of patients below the level of a chronic spinal cord transection and diminished on the side of an upper motor neurone lesion. It was diminished or absent on the same side as a cerebellar lesion. Initiation of a tonic contraction induced a postural 'red nucleus tremor' in a patient who had suffered a mid-brain thrombosis. Vibration-induced tonic contraction was normal in Parkinson's disease but was absent in two patients with dystonia.

The ability of the alpha anterior horn cell to respond phasically to a synchronous stimulus and tonically to asynchronous stimulation is discussed in relation to the influence of descending motor pathways.

This project was made possible by grants from The National Health and Medical Research Council (from the estate of the late Priscilla May Bowling) and the Post-Graduate Foundation in Medicine of The University of Sydney. Ciba Co. Pty. Ltd., Merck Sharp and Dohme Pty. Ltd., Sandoz Australia Pty. Ltd. and Smith, Kline and French Laboratories (Australia) Ltd. have given most generous financial support.

The figures for this paper were prepared by the Department of Medical Illustration, University of New South Wales.

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