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THE INFLUENCE OF AFFERENT AND DESCENDING PATHWAYS ON THE RHYTHMICAL AND ARRHYTHMICAL COMPONENTS OF MUSCULAR ACTIVITY IN MAN AND THE ANAESTHETIZED CAT

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A normal muscular contraction is never perfectly smooth, and frequency analysis of a myographic record shows that in general there is a regular rhythmical component (which in man is about 9 c/s; in the cat about 15 c/s) the mechanism of which seems to be based upon oscillation in the stretch reflex (Lippold, Redfearn & Vučo, 1957). There is also an irregular component in the frequency spectrum of muscular activity not dependent upon the stretch reflex, because it is still present after deafferentation (Perkins, 1945) and occurs in tabetics (Halliday & Redfearn, 1958).

It became apparent, during a study of the frequency spectra of various types of tremor (e.g. thyrotoxic tremor, emotional tremor, shivering, etc.), that this random element had a variable amplitude under different circumstances although the over-all tension in the muscle remained the same. Thus the random component could make up a varying proportion of the total strength of a muscular contraction.

In this paper, variability of the random element has been confirmed by comparison of the mechanical records of various types of muscular movement. These were shivering (in man and the cat), reflex contraction (in the cat), voluntary contraction (in man) and muscular activity resulting from electrical stimulation of the motor cortex of the cat.

METHODS

Human experiments

Production of shivering. Twenty-two young adult male subjects were made to shiver by stripping them naked and pouring cold water over them until they did so.

Recording apparatus. Tremor of the forefinger, and separately of the middle finger, was recorded

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at a voluntary tension of 50 g both in flexion and extension (separately). An R.C.A. 5734 mechano-electronic transducer was connected to a bending bar via a ball joint. The bending bar was attached to a stirrup for the finger (Fig. 1). One oscilloscope displayed the isometric tension so that the subject was able, by superimposing the two cathode ray spots, to maintain a steady tension of any desired value (50 g). A second oscilloscope working at greater amplification, with a time constant of 0·5 sec, was used to record the tremor photographically on film moving at 2·5 cm/sec.

Frequency analysis. The tremor record was used to modulate a 5 kc/s signal from an oscillator, thus giving a photographic record in the form of a black silhouette. This was enlarged eight diameters and printed on a continuous paper strip by means of an automatic printing machine.

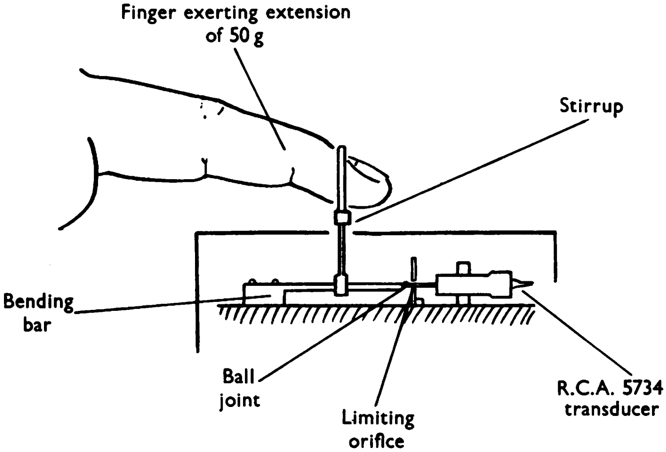

Fig. 1. The apparatus used for recording tremor of the forefinger. An electronic transducer is attached to a bending bar, the deformation of which is linearly related to the force exerted by the finger in the stirrup.

Lengths of tracing 125 cm long (representing about 6 sec duration) were attached to the periphery of a flywheel, 125 cm in circumference, which was rotated up to a speed of 1500 rev/min and allowed to slow down exponentially on its own, the process taking about 40 min. Lamps and photocells recorded the trace and a calibration mark. Resonant circuits fed by these energized two pen recorders. The principle of this method of frequency analysis has been described by Barber, Ursell, Darbyshire & Tucker (1946).

Animal technique

Shivering. Cats were lightly anaesthetized by an intraperitoneal injection of veterinary Nembutal (pentobarbitone sodium, Abbott) 25–35 mg/kg body weight and ether by mask if necessary. If the depth of anaesthesia was correct most animals shivered spontaneously or on slight cooling of the skin, provided that the body temperature was between 35° and 38° C. Shivering was arrested by warming.

Operative technique. The tibialis anterior muscle was prepared for recording by the method of Brown (1938). For cortical stimulation a trephine hole was made over the motor cortex. In some animals all the dorsal roots supplying the lower limb were divided.

Transducer and amplifiers. The methods of recording the tension of the tibialis muscle were described by Lippold, Redfearn & Vučo (1958). Frequency analyses of these records were made with an Ediswan analyser, the recordings being transcribed on to magnetic tape for storage purposes. This was achieved by a frequency modulation system (transitron-Miller oscillator to

modulate the signal; Eccles-Jordan trigger circuit feeding a diode-pump and integrating network for demodulation) because tape will not directly accept the low frequencies involved and amplitude modulation on tape suffers from an unduly high noise level when replayed (Fig. 2).

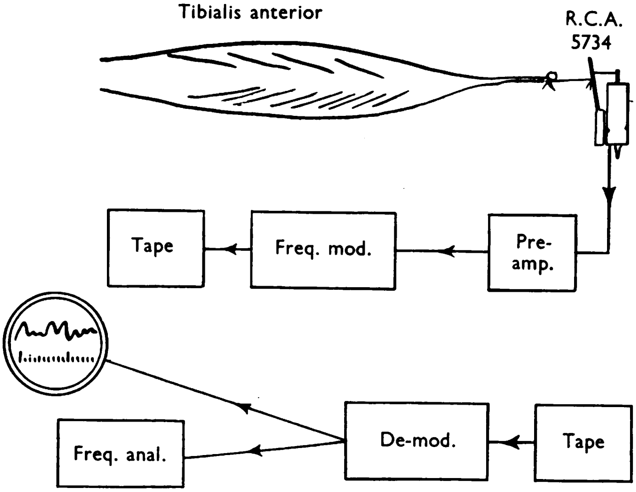

Fig. 2. **Block diagram of recording system used in the experiments upon tibialis anterior (cat). Storage on tape was necessary because the frequency analyser used in the animal experiments was housed elsewhere.**

RESULTS

Experiments in man. The subjects were required to maintain as accurately as possible 50 g tension during a voluntary contraction. This was done for 20 sec periods, under normal conditions and later during shivering. Thus the shivering records were the result of a combination of voluntary activity with that due to shivering. For purposes of this paper all the results have been pooled and are shown in Fig. 3, which gives the frequency spectra of normal voluntary contraction (N) and that of the same muscle when shivering (S). Since the conditions were isometric the Y axis represents force of contraction, while the X axis shows frequency. It is to be noted that in these spectra as frequency increases the amplitude of the frequency components falls off progressively. This is associated with the method of recording which does not allow free movement of the finger. When free movement of the finger is allowed and acceleration is plotted against frequency, the base level of the spectrum remains roughly horizontal. If, on the other hand, the spectrum is presented as a power spectrum, which is usual engineering practice, the Y co-ordinates are squared and the spectrum falls off with frequency even more abruptly than in the present case.

It can be seen from this graph that the shivering spectrum is generally similar to the normal one but that the amplitude is greater at all frequencies. The shivering curve shows the hump between 6 and 12 c/s which is well known to occur in the normal subject. This hump, which is associated with the stretch reflex, appears to be relatively larger in the shivering muscles.

Cat experiments. Figure 4 shows the frequency analysis of tension recordings from the tibialis anterior of an anaesthetized cat under different conditions. *C* is the activity due to cortical stimulation (at 75 c/s and of pulse width and

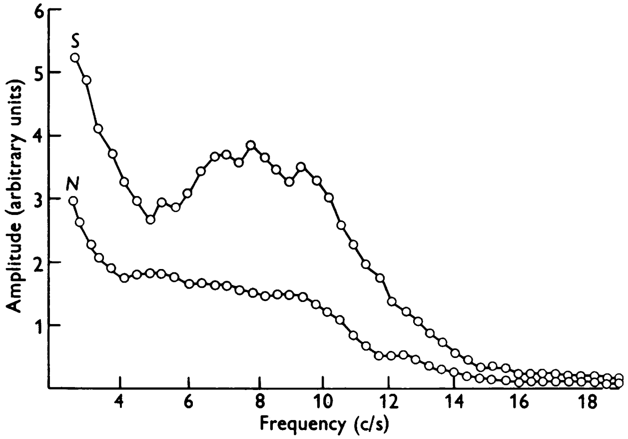

Fig. 3. Frequency spectra of tension records obtained from the middle finger exerting an upward tension (extension) of 50 g. *N* is the pooled results from 27 normal subjects. *S* is the curve obtained from 22 of the same subjects after shivering was induced. It represents the combination of activity due to shivering with that of voluntary contraction.

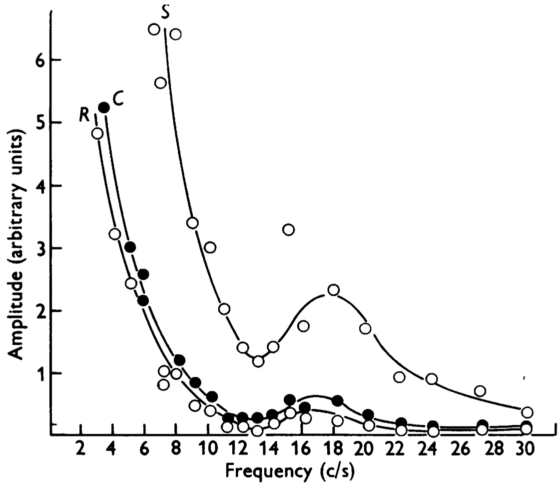

Fig. 4. Tibialis anterior, anaesthetized cat (sodium pentobarbitone, 35 mg/kg intraperitoneal). Frequency analyses of: *R*, sustained reflex activity produced by sensory stimulation of the same limb; *C*, cortical stimulation (pulses at 75 c/s; duration and voltage adjusted to maintain an approximately constant contraction strength); *S*, shivering activity. The mean tension during each of these three procedures was maintained at the same value.

voltage sufficient to give the required average tension); *R*, reflex contraction produced by appropriate pressure on the ipsilateral foot and *S*, shivering. The average tension produced by procedures *C* and *R* was adjusted in each case to be equal to that obtained in *S*, which depended upon heat transfer, body temperature, etc., but which remained fairly constant for 4–5 min periods.

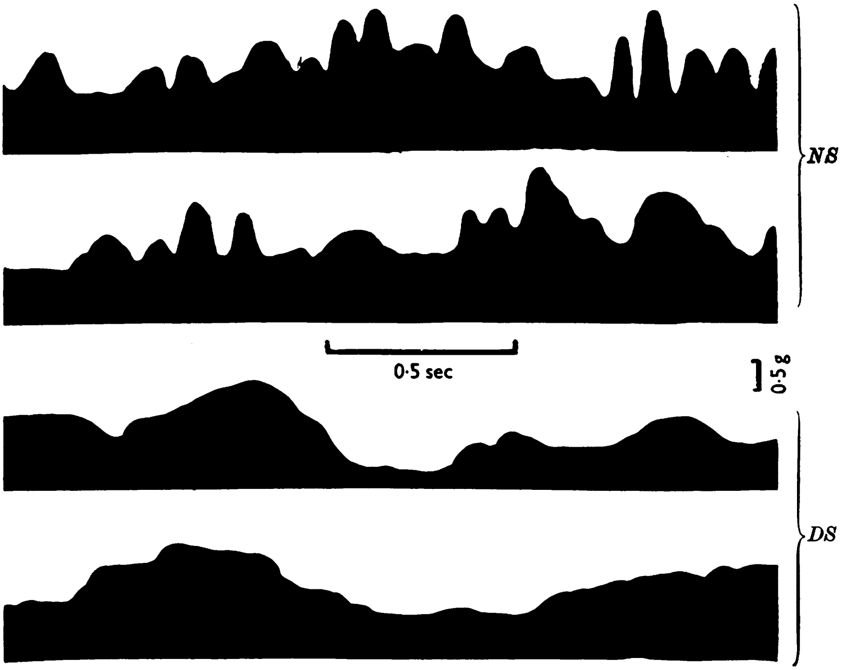

Fig. 5. Anaesthetized cat. Tension records from tibialis anterior. *NS*, during normal shivering. *DS*, 1 min after cutting the dorsal roots L5, L6, L7 and S1, on the same side.

Animals with intact reflex arcs gave results which showed that the overall tremor amplitude was greater at all frequencies when activity was due to shivering. Cortical stimulation and reflex activation produced much smoother contraction.

Fig. 5 shows the effect of deafferentation of a muscle which is shivering. When the dorsal roots L5, L6, L7 and S1 were cut on the same side, there was an immediate reduction in the amplitude of the shivering in tibialis anterior (and the remainder of the limb) and the tension record became irregular. After a short, variable delay, the amplitude regained its former level, but the regular oscillations due to the reflex arc had disappeared, leaving an irregular tracing.

This is confirmed by analysis (Fig. 6). After cutting the dorsal roots the regular activity at 15 c/s is absent. There is, however, still considerable activity in the muscle but of an irregular nature, spread over the whole frequency range.

In the deafferented muscle as in the normal, cortically induced contraction was smoother than the contraction due to shivering.

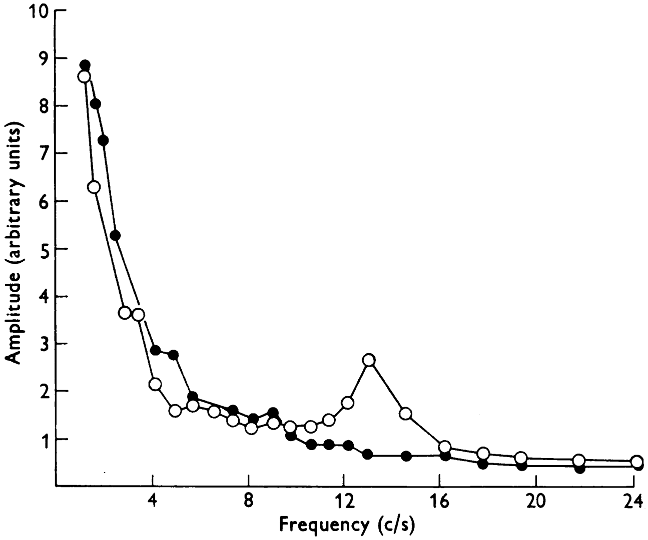

Fig. 6. Frequency spectra derived from the experiment of Fig. 5. Open circles, shivering before deafferentation. Closed circles, shivering after deafferentation. The hump at 15 c/s is absent in the second curve, but the irregular activity remains.

DISCUSSION

These experiments show that the tension in a muscle during shivering is produced by a more irregular contraction than is the case during normal voluntary activity. In both man and the cat the frequency spectrum of shivering has a greater amplitude at all frequencies than it has in the case of voluntary or reflex contraction. Thus, in shivering, for any given contraction strength, a greater proportion of the force produced is oscillatory in character; moreover this oscillatory activity is spread throughout the frequency range and not limited to 9 c/s.

The shivering frequency spectrum shows the hump (about 9 c/s in man; 15 c/s in the cat) which occurs in the normal spectrum of muscular activity and is associated with oscillating feed-back in the stretch reflex servo-loop. It appears to be relatively larger in shivering muscle, which suggests that gamma efferent activity is increased during shivering. However, the gamma system is not indispensable for shivering, as is shown by the fact that deafferentation does not abolish the random activity.

Perkins (1945) shows recordings from rabbit muscles which illustrate this point. They are of the muscular activity in the hind limb during shivering before and after deafferentation. Beforehand, the record shows a fairly regular rhythm at about 15 c/s, whereas after section of the dorsal roots the activity is irregular but not absent. We have submitted enlargements of Perkins's records to frequency analysis which confirms that the 15 c/s oscillations are removed on interrupting the reflex arc. Thus, after deafferentation, there is still shivering activity present, distributed over the whole frequency range.

As tremor amplitude is known to be proportional to the muscular force being exerted (Sutton, 1956), there is the possibility that shivering is solely due to increased alpha activity. In the intact limb, the simultaneous contraction of prime movers and their antagonists might generate the requisite heat without giving rise to external tension or movement and might be expected thus to produce an increase in tremor. Such a hypothesis could not, however, account for the major part of the muscular activity taking place in shivering, because our results have shown that (*a*) shivering can occur in tenotomized muscle, and (*b*) that for a given tension in a muscle (i.e. a given amount of alpha activity) the fraction of this tension due to tremor can vary; there is more tremor in a 50 g contraction due to shivering than there is in a cortical or reflex contraction of the same strength.

Birzis & Hemingway (1956, 1957*a*, *b*) have shown that a pathway proceeding from the posterior part of the hypothalamus, passing laterally and dorsally through the brain stem until it reaches the lateral columns of the spinal cord, is responsible for shivering in the cat. This also seems to be true in the human (Uprus, Gaylor & Carmichael, 1935). Destruction of this tract abolishes shivering, stimulation causes it and electrodes placed in the tract give evidence of electrical activity during shivering. For a review of the evidence concerning these pathways see Birzis & Hemingway (1956).

The mechanism by which activity in this tract gives rise to shivering is not yet known. Birzis & Hemingway claim that the impulses going down the pathway are not timed in a manner which could account for shivering but constitute a steady stream of activity. They conclude that the muscular oscillations are produced at a spinal level through the action of the stretch reflex, but, as we have demonstrated, the presence of the stretch reflex is not necessary for shivering to occur. Nor is the amplitude of the oscillations merely a function of the tension developed in the muscle due to the activity of the alpha motoneurones. Thus shivering cannot be explained solely on the basis of increased muscular tone or increased reflexes or a combination of the two.

A smooth muscular contraction must be the result of random activity of motor units. Loss of this smoothness might arise in several different ways. (*a*) If the tract concerned with shivering is composed of a number of fibres which is small relative to the number of innervated motoneurones, synchronization would be expected to occur. Thus one descending fibre would drive several motoneurones synchronously. A tract composed of a relatively large number of fibres such as the pyramidal tract, would not, on the other hand, be likely to give rise to this effect. (*b*) In shivering, the descending impulses might originate synchronously, although this possibility seems unlikely in view of Hemingway's results. (*c*) Synchronization can arise in the motoneurone pool. It is known that damage to anterior horn cells causes synchronous firing (Buchtal & Madsen, 1950) and there is some evidence that this factor is responsible for the irregular tremor of mercurialism (Isch, Rohmer & Marx, 1950) and that of poliomyelitis (Fessard, Léfébvre & Lérique, 1948). A similar motoneurone synchronization could be brought about by spreading inhibition or excitation within the pool, for instance, as a result of inhibition by Renshaw cells (Renshaw, 1941) which could be activated via the shivering pathway.

SUMMARY

1. The frequency spectrum of shivering in man was compared with that of normal muscular activity. The results show that the rhythmical and arrhythmical components are of greater amplitude during shivering, although the tension in the contracting muscles was the same.

2. In order to show that this effect was not simply due to an increase in antagonistic activity without the production of external tension, comparison was made in the isolated tendon of m. tibialis anterior of the anaesthetized cat of shivering, reflex activity and activity resulting from stimulation of the motor cortex.

3. In animals with intact reflex arcs, results similar to those in the human were obtained. When the afferents from the hind limb were cut, the arrhythmical component remained greater in shivering than in cortically induced activity at the same tension. The rhythmical component was abolished because this was due to self-oscillation in the reflex loop.

4. Hypotheses to account for the increased irregular activity found in shivering are discussed and it is shown that shivering cannot be due merely to increased alpha activity, gamma activity, or a combination of the two.

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