AN INVESTIGATION INTO MUSCLE TONE USING PRINTED MOTORS AS TORQUE GENERATORS

by

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ABSTRACT

Forces have been applied to the wrist joint in man by means of printed armature motors driven by a wave-form generator. The resulting movement of the limb has been recorded and analysed. On occasion other joints were investigated. This approach permitted an analysis to be made of joint and, more importantly, muscle response to applied force. In the relaxed state the response of muscle to applied force may be described as resting muscle tone; and it is with investigation of this parameter that this study has been principally concerned. Further information about the response of the muscles has been obtained by EMG recording. The applied force wave-form took three main forms.

In the first part of the investigation the applied wave-form was sinusoidal and swept in frequency from 0.5 to 20 Hz. The amplitude of the wave-form could be altered. This permitted investigation of the resonant frequency of the limb. It has been shown that the response of the limb is non-linear; that is, it is stiffer for small forces than large ones. The form of this non-linearity has been determined for a number of subjects and a sex difference has been found.

A new technique involving the measurement of wrist compliance by the application of amplitude ramped low frequency (1 Hz) square wave torque pulses has been evolved. This has been used to confirm the form of the non-linearity and the sex difference. By biasing the system it was shown that the non-linearity is not caused by pretensioning of the musculature, as had been suggested by similar work on the extra-ocular muscles of the dog. A limited investigation of the effects of muscle cooling on wrist compliance has been carried out. Cooling has been shown to reduce considerably the compliance of the wrist and this is associated with a reduction in electromyographic activity. This decreased compliance has been shown to be abolished temporarily by active or passive movements of the system. The effect of active and passive movements has also been investigated at physiological temperatures.

Using a low amplitude sinusoidal or square wave torque of approximately 3 Hz it has been shown that the compliance of the the system is heavily dependent on its prior history; it may be said to behave thixotropically. The significance and possible causes of this thixotropy are discussed.

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1) INTRODUCTION

1.1) The History of Muscle Tone

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"Tonus - id est vigor" (Matthew Sylvaticus, 1480)

1.1) THE HISTORY OF MUSCLE TONE

1.1)1 The phenomenon of tone.

Physiological tone, or tonus, is defined (O.E.D.) as "the degree of firmness or tension proper to the organs or tissues of the body in a strong and healthy condition". The word tonus is derived from Tovos which the ancient Greeks used to describe the tension of a tuned string. Muscle tone is now understood to be the resistance demonstrated by a relaxed muscle in response to passive lengthening.

The early natural philosophers of ancient Greece had no conception of muscle physiology as such; no distinction was made between muscles and the flesh, and: "They had no idea whatever of the share of the muscles in voluntary movement, but at once tried to find the deeper cause of it in Pneumatism" (Bastholm 1950). Plato and Aristotle attributed to muscles: "so trivial a use as to think that they kept out heat in summer and cold in winter" (Vesalius vol i p182 cited by Todd 1847).

By the end of the classical period and the time of Galen of Pergamon (129-201) knowledge of anatomy and physiology had increased considerably. Galen was an empiricist and may be said to have founded the modern scientific method; it is an irony that his methods were not adopted, and his writings were to serve as medical doctrine for thirteen centuries or more. Galen identified muscles as the prime movers of the body, and he divided them into two categories - those that are inserted into bones or soft tissues by means of tendons, and those that are without tendons. He believed that when present the tendon itself possessed contractile properties and it was not until the time of Steno in 1660 that this theory was discredited.

Galen showed that if a flexor muscle was divided the limb automatically moved into extension under the pull of the antagonising extensor muscle. He concluded from this that there is a kind of tension between the muscles, the natural tendency of the muscle to contract being checked by its antagonist. This demonstration, that all movements of the limbs stem from contraction of individual muscles and that relaxation is a passive process in which the muscle is stretched back to its original state by an antagonising muscle, was a great leap forward; it had previously been believed that some muscles were capable of movement in up to six different directions. The operation of muscles in opposing pairs, and the natural tendency of the muscles to contract may have suggested to the Greeks that in health there was a state of tension observable in the muscles even in the absence of voluntary movements. Sherrington (1940) has suggested that when they spoke of the tone of the muscles: "They had in mind the mild grade of steady action of our muscles when for instance they simply maintain a posture".

In the seventeenth century the word "tonus" became imbued with quite a new meaning and this sowed the seeds of a confusion that persisted for nearly two hundred years. Friedrich Hoffman (1660-1742) believed that a ubiquitous aether-like fluid travelled via the brain and nerves, and placed all the tissues of the body in a state of partial contraction, and also maintained the fluids of the body in"that motion which was a condition of the preservation of life". Life to him consisted of the various tensions, or Tonus, of all the fibres of the body and of the movement of the blood. An excess or a deficiency of tonus compromised life, and could be combated by a "Tonic". These views were expressed in his treatise "Medicine Rationalis Systematicae" which appeared in 1729. The animist, Stahl, had earlier expressed similar views in his dissertation "Dissertatio de Motu Tonico Vitali" (1708).

By the time of Johannes Müller, Professor of Physiology at Bonn and Berlin, and one of the father figures of modern physiology, the meaning of tonus had subtly changed and had come to refer only to a type of "insensible contraction" to be found in the walls of blood vessels. Thus, in his "Elements of Physiology" (1840) Müller states: "They (arteries) possess a vital property of gradual, not periodic contraction, tonus. This is admitted by Parry, Weber, and Tiedmann ....".

Tiedmann (1834) had expressed his views on tonus remarkably clearly.

"These phenomena of contraction which are remarked in very many non muscular living tissues have been regarded by some physiologists as the pure effects of elasticity. But the proof that they ought not to be referred to such a cause is their disappearance immediately or very shortly after death. Other physiologists see in them the effects of muscular contractility. To this hypothesis it may be objected that the contraction is not determined by the same stimulants as these which induce it in muscular tissue, and that it is not accompanied as in the latter case, with oscillations followed by a palpable extension. Several physiologists who distinguished the movements perceived in these tissues as well as from the effects of elasticity as from movements produced by muscles, regard them as specific vital phenomena and give them the name of tonic movements; the force which produces them they call tone, tonicity, and insensible organic contraction .... by the same name (tonus) it is mentioned by Whytt, Cullen, Bordea, Grimaud, Barthez, Chaussier and others. Blumenbach called it tonicity or contractility of cellular tissue."

It is ironical that many years before, John Hunter, unaided by microscopic evidence, had concluded correctly that constriction of the arteries was brought about by muscular contraction. Thus, for

Müller and his contemporaries, tonus was a property peculiar to arterial walls, not found in other tissues. Despite this, Müller is frequently cited as the first physiologist to describe skeletal muscle tone, for example Pollock (1928), Paskind (1932) and Noël (1973). Müller did, however, describe what would now be called tonic activity in the skeletal muscles:

"The living muscles must not, however, be supposed to be at any time in a state of complete relaxation. They are constantly even in the state of rest, subject to the influence of the nervous principle, this is seen in the retraction of divided muscle, in the slight tremors of muscles laid bare during life, and the dislocation of the features and the drawing of the tongue to one side in hemiplegia". (Müller, 1842).

Galen had used virtually the same words seventeen hundred years earlier. Neural contribution to muscle tone was investigated by physiologists during the latter half of the nineteenth century, and it was in this period that the term muscle tonus assumed its present meaning.

Brondgeest (1860) showed that when the hindlimb of the frog was allowed to hang freely the length of the flexor muscle was slightly increased when the afferent roots of the sciatic plexus were severed. Earlier experiments had failed to show any lengthening following section of nerves - this work was reviewed by Heidenhain (1856). One exception was Marshall Hall, who in 1836 had shown that muscular tension was dependent on an intact spinal cord. Wundt (1858) observed muscular lengthening following section of its motor nerve, but he hesitated to ascribe it to anything more than an after effect of the contraction induced by cutting the nerve.

Tschiriew (1879) obtained a muscular lengthening after motor nerve section; von Cyon also reported lengthening following sectioning of the afferent nerves.

Von Anrep (1880) repeated Wundt's experiments and demonstrated that normal tonus was dependent on intact efferent and afferent nerves.

Thus, by the late nineteenth century, muscle tonus had been generally accepted as a neurally reflexly mediated phenomenon, dependent on intact peripheral nerves and spinal cord. This view is expressed in the many Physiology textbooks of the day, for example, Kirkes Handbook of Physiology, 1876:

"This kind of tone must be distinguished from that mere firmness and tension which it is customary to ascribe under the name of tone to all tissues that feel robust and not flabby, as well as to muscle. The tone peculiar to muscles has in it a degree of vital contraction; that of other tissues is only due to their being well nourished, and therefore compact and tense."

This reflex theory was to receive an enormous impetus from Sherrington and his co-workers in the late nineteenth and early twentieth centuries.

1.1)2 Sherrington and "reflex posture."

Sherrington is principally known for four fundamentally important discoveries. Firstly, his rediscovery and refinement of the decerebration technique (originally described by Magendie in 1823). The second and third discoveries are the result of his painstaking research on reciprocal inhibition, and are the ipsilateral flexion reflex and the crossed extensor reflex. These reflexes are elicited by painful cutaneous stimulation. The fourth discovery, and possibly the one for which he is best known, is the stretch reflex. Sherrington's early research concerned the investigation of muscle sense organs. The best contemporary histological descriptions of muscle sense organs were those of Sherrington and Ruffini. Sherrington was aware of the earlier work of Brondgeest (1860) in which reflex tone had been described in a skinned frog, and he shared Brondgeest's view that the afferent information came from the muscle itself. In 1894 he published a paper: "On the anatomical constituents of nerves of skeletal muscle" where he described the sensory nature of the muscle spindle and tendon organ. Sherrington (1893) and Mott and Sherrington (1895) showed that when a limb is rendered anaesthetic by severance of all its afferent roots the muscles feel peculiarly limp and flaccid and the passive mobility of joints is greater than normal. This increased passive mobility is "due to loss of tonus (hypotonia) in the limb muscles" (Sherrington, 1900). Sherrington stressed that not all skeletal muscles habitually possess such a tone, and that it may not be present in all muscles at all times. When the elbow is well flexed the biceps are so slack as to feel toneless: "It may be that the neural tonus of skeletal muscles is only present in them so long as they are stretched, and that the tension developed in the muscle by its contraction excites reflexly in it a condition of tonus" (Sherrington ibid).

The classical paper on the stretch reflex was published by Liddell and Sherrington in 1924. This paper showed unequivocally the contribution of the intact nervous system to muscular tonus. In contrast to the other two reflexes the stretch reflex was specific, that is, it affected the muscle being stretched only, although there might be a decrease in the threshold for stimulation of its synergists. In the decerebrate animal, two distinct phases could be distinguished: an initial large phasic response followed by a steady lower level tonic response. This was the neural basis of muscle tone, or "reflex posture" as Sherrington preferred to call it. Sherrington was also able to demonstrate inhibition of the stretch reflex with stimulation of an ipsilateral antagonist afferent nerve or by excessive stretch of the muscle which elicited a sudden decrease in muscle tone - the clasp-knife reflex.

Sherrington (1909, 1913) had noted that extensor muscles in decerebrate preparations possessed the property of "plasticity", that is, they were able to exert the same tension at different lengths, in the manner of smooth muscle. Thus, if the rigid muscle was forcibly lengthened or shortened, it would remain at its new length for some time. To distinguish this property from the clasp knife reflex which was also observed following forcible lengthening Sherrington named it the "lengthening reaction". The opposite effect which followed imposed shortening, he named the "shortening reaction".

The influence of head, neck and vestibular mechanisms on this type of preparation was studied by Magnus, de Klein and Camis, and the superficially similar rigidity produced by decerebellation in animals was investigated by several workers, notably Sherrington himself and Pollock and Davis.

Earlier work on the vestibular organs and the cerebellum had been carried out by Ewald, and Flourens and Luciani respectively.

Sherrington originally (in the "Integrative Action of the Nervous System") thought that there were two separable systems of motor innervation, one tonic and the other phasic.

Gotch (1896) had shown that the latency of the kneejerk is shorter than indubitably proven reflexes and that it consists of a simple twitch rather than a tetanic contraction, which he held to be indicative of a reflex. Sherrington (1906) debated whether the kneejerk and the mechanisms responsible for maintaining the tonus of the knee extensor are the same phenomenon. He observed that the one is dependent on the other, if there is no tonus there is no kneejerk, and "its briskness varies pari passu with the degree of this tonus." He concluded that there are separate phasic and tonic systems of motor innervation.

> "Two separate systems of motor innervation appear thus controlling two sets of musculature: one system exhibits these transient phases of heightened reaction which constitute reflex movements; the other maintains that steady tonic response which supplies the muscular tension necessary to attitude."

This view, that there were two separate anatomically distinct systems controlling long and short term aspects of muscle tone, enjoyed a brief popularity and the tonic system became identified with the physiological extensor muscles which counteracted gravity, whereas the phasic system chiefly comprised the flexors. Sherrington was therefore making an implicit distinction between movement and posture. In later years, this distinction became less tenable and Sherrington ceased to emphasise it. Later workers have stressed that the two are inseparable: "Posture accompanies movement like a shadow" (Hunt) and: "they coalesce and often cannot be separated" (Cobb). (Both cited by Granit, 1966).

It was known that muscles possessed a sympathetic innervation, and a few workers attributed to this the role of the maintenance of tone (Hunter, 1925). This dual innervation theory received little support and was discredited by Kuntz and Kerker (1926). Ranson (1928) believed that tonus was maintained by antidromic impulses in the dorsal roots.

Further information on phasic and tonic responses was to come from workers who examined the individual components of the reflex arc. Many of these workers had been strongly influenced by Sherrington.

1.1)3 The components of the reflex arc.

The stretch reflex is a functional entity which Sherrington had shown to be a basic mechanism in the maintenance of tone in postural antigravity muscles. Although Sherrington did not use the term it may be considered as a feedback system which consists of three parts:- an error detector, a controller and an effector. The error detectors are the muscle spindles and tendon organs which respond to changes in length or tension. The effector is the skeletal muscle, which is a tension generator. The controller is formed by synaptic connections between the error detectors and the effectors; these lie in the spinal cord and it is here that other sensory and motor influences from associated parts of the nervous system may be exerted.

1.1)4 The error detectors.

The muscle spindles seem to have been originally noticed by Hassal in 1849. Kölliker (1863) and Kühne (1863) provided a fuller description, and Kühne gave them their name. Their sensory nature was demonstrated by Ruffini in 1898, who also showed that the spindle had two different types of sensory nerve ending. The larger, more obvious nerve ending is found coiled round the central swollen part of the spindle so he named it the "annulospiral" ending. The other ending, when present, is also found in the equitorial region of the spindle; in this type the nerve divides into several fine branches and because of this appearance he named it the "flower-spray" ending.

Sherrington (1894) traced the majority of these nerves to the spinal ganglia; here was proof of their sensory nature. Sherrington also introduced the term "intrafusal" to describe the muscle fibres (2 to 20 in man) of which the spindle was composed. The ordinary muscle fibres, which were somewhat larger, he named "extrafusal". Intrafusal muscle fibres were shown by Sherrington to have motor end plates, but in 1930, when with Eccles he published a paper describing two characteristic groups of fibres in the ventral roots, he appears to have believed that all these fibres were destined for extrafusal end plates as he divided the total isometric tension of the muscle by the number of nerve fibres in order to form an estimate of the average tension value of an individual motoneurone in different muscles (Granit, 1966).

This problem was later taken up by Leksell (1945), who was able to show that stimulation of a number of the smaller fibres produced no discernible contraction in the muscle. Moreover, he was able to show that stimulation of the small motor nerves produced a discharge in the sensory nerves from the muscle spindles, if the muscle was initially stretched. It therefore became clear that this group of small nerves must supply only the intrafusal muscle fibres, and that contraction of the intrafusal muscle fibres must increase the sensitivity of these receptors. This discovery had been anticipated by Rossi in 1927 and Matthews in 1933. Leksell showed that the conduction velocities of the larger fibres classified them as the alpha group of Erlanger and Gasser (1937) and the smaller ones belonged to the gamma group. These gamma fibres have been more recently named the "fusimotor" fibres (Hunt and Paintal, 1958). Matthews (1933) showed that the muscle spindles lie effectively in parallel with the extrafusal fibres, contraction of the muscle therefore "unloads" the spindle, and it stops firing - unless there is a concomitant discharge in the fusimotor fibres. This observation suggested that muscle could be activated in two ways: either directly via the alpha motoneurones, or indirectly via the fusimotor fibres. Activation of the fusimotor fibres would cause the intrafusal fibre to contract, the resulting stimulation of the muscle spindle would, reflexly via the alpha motoneurones, cause the muscle to contract and to match the length of the intrafusal fibre, Eldred, Granit and Merton (1953); Merton (1953); Granit, Holmgren and Merton (1955). This was given the name of "the follow-up length servo" by Hammond, Merton and Sutton in 1956.

It therefore seemed that Sherrington's concept of "a final common pathway" required some revision; skeletal muscle could be induced to contract by centrifugal impulses in the alpha or gamma systems. The relationship between the two systems and the degree to which they cooperate has been extensively investigated by a number of workers in the last three decades. This field has been extensively reviewed by Granit (1970).

An early concept was that of Granit et al. (1955): "It is probable that posture would employ the gamma route, and that rapid movements with minimum time go through the alpha route." This follows on from the premise that impulses in the alpha motoneurones will serve to generate changes in muscular tension, whereas impulses in the gamma motoneurones will serve to generate changes in length. It is therefore possible to speak of a "gamma bias" which will maintain the length of the muscle independent of tension.

This concept has been consistently questioned by Matthews (1959, 1972) who believes that the gain of the stretch reflex is insufficiently high to act as a servo that maintains length in the face of tension challenges. Three observations at least stand in its favour. Firstly, when a maximally contracting muscle is released, there is a silent period as the spindles are unloaded. This illustrates that, under some circumstances at least, the spindles can command a large proportion of the motoneurones. Secondly, Marsden, Merton and Morton (1976) (A) have recently shown that the gain of the stretch reflex is variable from a value of zero to a high value. Thirdly, Granit (1970) has observed that the separation of alpha and gamma functions in higher animals is scarcely likely to have evolved unless it confers an advantage on the organism.

However, most authorities are agreed that in "normal" movements coactivation of the alpha and gamma systems is the rule.

More recently study of the muscle spindle has revealed further complications in its structure. Barker (1948) renamed the annulospiral and flower-spray endings the primaries and secondaries respectively, and pointed out that the afferent nerves of the secondary endings were on average smaller than those of the primaries. The capsule of a muscle spindle normally contains a number of intrafusal fibres; Cooper and Daniel (1956) and Boyd, in the same year, distinguished a different type of intrafusal fibre in man and in the cat respectively. In the familiar type of intrafusal fibre, the swollen equitorial region possessed a nuclear bag containing a jumble of nuclei, but in the new type there was no equitorial bag, and the nuclei were arranged in a linear chain. These were called nuclear chain fibres to distinguish them from the familiar nuclear bag fibres. They appear to be most numerous in muscles capable of finely controlled movements (Granit, 1970).

In 1962 Boyd, using de-afferented muscle spindles, was able to show that the efferent gamma fibres ended on the muscle spindle in two different ways. One type of ending was the large motor end plate in the polar region of the intrafusal fibre, the other type penetrated further into the equitorial region and terminated as a diffuse network in which small end plates could be distinguished. These two types of termination have been named the gamma plates and gamma trails respectively. There is presently controversy regarding the distribution of these two types of ending; Boyd and his group state that, in some muscles at least, nuclear bag fibres are innervated by gamma plates and nuclear chain fibres by gamma trails, but Barker and his group (for example, Barker, 1967) have found many exceptions to this, and have shown that some nuclear bag fibres may possess both types of fibre. In the same paper, Barker has described a third type of efferent ending which lies towards the distal end of the polar region and is indistinguishable from the extrafusal endplate. This "Type I" receptor may be innervated by a branch of the alpha motoneurones, an arrangement that is common to the all intrafusal fibres in amphibia.

The tendon organs, which comprise the other class of error detectors, are rather simpler in organisation. Golgi (1903) appears to have been the first to describe the tendon organ that now bears his name. This receptor is found in the region between muscular and tendinous tissue and is often associated with other smaller corpuscles resembling Pacinian touch receptors. Poláček (1966) has reviewed the senory structures in tendons and ligaments. The Golgi tendon organ is usually connected to a bundle of ten or so extrafusal fibres which may belong to different motorunits; it receives no motor supply and its afferent connections are mediated by large Ib fibres (Barker, Ip and Adal, 1962).

The mechanical arrangement of the two types of receptor is different. The spindle is in parallel with the extrafusal fibres, whereas the tendon organ is in series (Fulton and Pi-Suner, 1927-1928). Passive stretch will therefore load both structures, but active contraction will load the tendon organs and unload the spindles. It was at one time believed that the threshold of the tendon organ was rather high and that it functioned only as an "overload" detector, but more recent experiments have shown that in the cat soleus it will respond to a twitch in as few as fifteen motorunits. As each tendon organ is connected to a number of different motorunits this demonstrates that it has a low threshold (Jansen and Rudjord, 1964).

The physiological response of the spindles and tendon organs has been the subject of an enormous amount of research; only the briefest summary can be given here. The subject has been extensively reviewed by Granit (1970).

The response of the muscles to stretch has been studied in the absence of fusimotor discharge by using a drug such as a cocaine derivative or alcohol which selectively blocks the smaller gamma fibres in the motor nerve (for example, Matthews and Rushworth, 1957). In this type of preparation the primary endings respond to stretch with an initial burst of firing which rapidly declines to a lower steady value. These two phases are generally described as dynamic and static respectively and they indicate that the primary ending is responsive to both position and velocity.

The secondary endings are only slightly responsive to the velocity of stretching; their maximal response is to steady stretch, they therefore serve as length detectors (Cooper, 1959). The static threshold for primary and secondary fibres is similar. The response of primary and secondary intrafusal fibres is modified by gamma discharge. If individual gamma fibres are stimulated, two types of effect can be distinguished: in one, the static response to stretch is enhanced, and in the other the dynamic response is increased. The types of gamma fibre producing these effects are called static and dynamic fusimotor fibres respectively; they are not anatomically distinguishable, although the static fibres may be smaller than the dynamic. The relationship of static and dynamic fibres to the plate and trail endings is not known with certainty, but dynamic fibres appear to act on nuclear bag intrafusals and static fibres on nuclear chain intrafusals.

The response of tendon organs is to tension, but they may also be sensitive to the rate of stretching (Matthews, 1933).

Sensory structures in the joints and ligaments do not contribute to involuntary motor control; this was first demonstrated by Goldscheider (1889) and has subsequently been confirmed.

1.1)5 Muscle

The extrafusal fibres are the effectors in the servo loop; even with considerable gamma bias the tension developed by the intrafusal fibres is negligible. Two types of mammalian extrafusal fibres can be distinguished-ones which appear reddish and ones which appear pale (white). This difference in appearance has been known from early times, but to Ranvier (1874) belongs the credit for demonstrating that the contraction time of red muscle is longer than that of white. The historical aspects of this discovery and other aspects of muscle biochemistry have been reviewed by Dorothy Needham in her book "Machina Carnis" (1971).

This division of fibre types was known to Sherrington; his collaborator, Denny-Brown, (1929) showed that the slowly contracting red muscles are generally deeper lying and more easily demonstrate stretch reflexes. In mammals the extrafusal fibres all respond to a nerve impulse by means of a twitch; this is in contrast to the prolonged graded contraction which is produced by the "tonus bundles" which are present in the muscles of amphibia and mollusca. The innervation of extrafusal muscles is by a motor endplate; the motor axon divides into a number of terminal branches which are distributed onto a considerable number of muscle fibres. An action potential in the motor axon will depolarise all the muscle fibres to which it branches; this is the quantum unit of muscular action and was named the "motor unit" by Sherrington's group (Creed et al., 1932).

The extrafusal fibres supplied by one axon are not adjacent but are generally intermingled throughout the muscle. The number of muscle fibres per axon is known as the innervation ratio and is generally lowest in muscles that produce finely controlled movements. It was shown (Hay, 1901; Eccles and Sherrington, 1930) that the slower red fibres are associated with slower, smaller axons. Rexed (1944) has pointed out that generally the smaller axons come from smaller ventral horn cells. Buller, Eccles and Eccles (1960) showed that by transposing the nerves to a slow and a fast muscle in young kittens, a slow muscle (soleus) developed as a fast muscle, and a fast muscle (flexor hallucis) developed as a slow one. Recent evidence has suggested that a "trophic" substance is transported down the axon and acts on the muscle cell to modify its speed of contraction and its anaerobic capacity; it has also been shown (Salmons and Vrbová, 1967) that continuous tonic bombardment of a muscle fibre may slow its contraction time.

1.1)6 Spinal cord: motoneurones.

The information processing that is performed within the spinal cord, and the relationship between sensory and motor neurones there, are exceedingly complicated and imperfectly understood. Only a few leading ideas can be presented here. The subject has been comprehensively reviewed by Granit (1972).

The motoneurones that innervate the intra and extrafusal muscle fibres lie in the ventral horn of the spinal cord. They are very numerous, for example the L7 ventral horn of the cat contains 6000 cells (Henneman, 1974). The motoneurones associated with one muscle are said to form a motoneurone "pool".
A vast number of inputs converge on this pool; some of the largest

alpha motoneurones may each have 10,000 synaptic knobs on their soma and dendrites. The size of the alpha cells is variable, the largest cells have the largest axons (Ramon y Cajal, 1909), and these innervate the largest, fastest muscle fibres. Are these therefore phasic motoneurones? Granit, Henatsch and Steg (1956) investigated this theory using extensor muscles and showed that small motoneurones discharged repetitively in reflex response to stretch, whereas larger motoneurones responded only with a phasic burst of firing.

However, other workers have challenged the existence of separate groups of tonic and phasic motoneurones. Principal among these is Henneman, who claims that motoneurones are recruited simply in order of increasing size (Henneman's size principle). Experiments in which a variety of stimuli were employed on flexor and extensor motoneurones showed that their excitability is an inverse function of their size, and their threshold for inhibition is in direct proportion to their size (Henneman, Somjen and Carpenter, 1965a, 1965b).

Desmedt has demonstrated that the order of recruitment of motor units, and therefore motoneurones, is the same in slow movements and fast ballistic movements. This implies that it is unlikely that there are "tonic" motoneurones (Desmedt and Godaux, 1977, 1978).

Sherrington conceived of a neuronal pool as a population of homologous tonic and phasic motoneurones supplied by selectively distributed afferent inputs. Because of these different categories of input, the pool was "fractionated"; cells in the "discharge zone" were stimulated and the others formed a "subliminal zone" which was excited but not fired. "Facilitation" occurred when the subliminal zones due to different inputs overlapped giving an enhanced output; conversely, when discharge zones overlapped "occlusion" occurred and the output was decreased. A more modern view is that the inputs to a motor pool are more or less less equally distributed; fibres fire or not depending on their excitability (smallest first).

If the input to the pool increases, then larger cells are "recruited". The rate of firing of recruited motoneurones is either an inherent feature of the neuron, or it may be regulated by recurrent inhibition which is provided by Renshaw cells. The Renshaw cells themselves are subject to sensory input. Small neurons that have been recruited therefore fire continuously (tonically) and larger borderline ones that make the transition from the subliminal pool to the discharge zone will fire phasically. The response to an inhibitory input is the same as a decrease in excitation. The smallest fibres are therefore discharged much more frequently than the large ones, and motoneurones do not belong to fixed tonic or phasic types. Henneman (1974) has pointed out that the metabolic consequences of action potentials in the large fibres which innervate the large fast muscle fibres are much greater than that due to activity in the small ones.

At present,it is not certain whether "tonic" or "phasic" motoneurones exist - it is possible that they may exist in some species but not in others.

The cell bodies of the gamma fibres are found scattered amongst the alpha motoneurones in the ventral horn. In contrast to the alpha motoneurones they are tonically active and make no monosynaptic connections with afferent fibres. It is possible that as the gamma cell bodies are smaller than the alpha motoneurones they are more excitable and therefore most likely to be first discharged. However, they are not monosynaptically activated and the conduction velocity of their axons is quite low, so intrafusal activation is unlikely to precede extrafusal. There is, however, much evidence that in many circumstances parallel activation of the two systems occurs (Hunt, 1951; Kobayashi et al., 1952; Granit and Kaada, 1952).

1.1)7 Spinal cord: sensory cells and interneurones.

The bodies of the sensory cells lie in the dorsal ganglia and all sensory nerves enter the spinal cord through the dorsal roots. At any segmental level there are typically twice as many sensory fibres as motoneurones. The central ends of dorsal fibres divide into a number of branches which are distributed to higher centres and to various parts of the same and other segments. In a spinalised animal any sensory stimulus can elicit a reflex response; this shows that all sensory neurones ultimately make connections with motoneurones. Only the Ia afferent nerves from the primary endings relay directly (monosynaptically) onto the motoneurones. They relay onto the motoneurones of the muscle of origin, synergistic group, and possibly onto the motoneurones of antagonists. This latter monosynaptic inhibitory connection has been challenged by Eccles on the grounds that a single neurone is unlikely to act in an excitatory manner on one postsynaptic cell and an inhibitory manner on another (Eccles, Fatt and Landgren, 1956). (This is an extension of Dale's principle that any neurone releases only one transmitter substance). The motoneurones of the muscle of origin and the synergistic ones form a myotatic unit.

All other sensory fibres relay via one or more interneurones; the spinal cord contains a vast number of interneurones (375,000 at L7 in the dog, Gelfan (1963), greatly outnumbering other sensory and motor cells. The interneurones act as amplifiers, pulse stretchers, modulators and inverters. Group II fibres from the spindle secondaries operate through a multineurone arc and it has been shown that Ib fibres relay through a single interneurone; they thus form a disynaptic three neurone arc.

Influences from higher centres may be exerted on the interneurones comprising the reflex arc (Lloyd in the cat (1941)), or may be directly exerted on the motoneurones (Bernhard, Bohm and Petersen, 1953).

1.1)8 Neural and muscular contributions to muscle tone.

A muscle at rest, in the absence of "willed" movements or imposed loads, will be metabolically quiescent and electrically silent. This has been confirmed by Ralston and Libet (1953), Basmajian (1967), and many others. Despite this, the view that all the muscles of the body are permanently in a mild state of tetanic contraction is still sometimes encountered, for example, Schmidt (1978): "even in a relaxed limb, the motor nerves are activated at low frequency. The resultant tone is detectable as a resistance to passive bending of the limb."

Under some circumstances, an apparently resting muscle may exhibit a resting tonic discharge; this is because the weight of the animal or the limb subjects the muscle to the force of gravity, and the muscle, thus stretched, reflexly contracts. This mechanism, which automatically counteracts the force of gravity, is invaluable in the maintenance of posture; it can operate without any higher control and is therefore present in chronically spinalised animals. In the intact animal this basic reflex is supplemented by others which come from different spinal levels and from brain structures. Thus the long spinal reflexes, flexion reflexes, crossed reflexes, and the head and neck reflexes are all very important in the provision of an appropriately distributed pattern of muscle tone.

In a standing, stationary animal, it would appear that maintenance of muscle length would be the most important controlled variable, and there is much evidence to suggest that regulation of this system proceeds through the fusimotor system which "sets" the length of the muscles. In a decerebrated animal, fusimotor discharge is much increased and the muscles become set at a shorter length, producing an exaggerated caricature of normal standing. Because of the extra gamma bias the spindles fire even in the absence of applied stretch. The resistance to stretching of the muscles is therefore greater than normal, although this increased tone is confined to the physiological extensors which counteract gravity. It has been shown that in the sloth, an arboreal animal which lives "upside down", the increased tone is found in the flexors. This "myotatic reflex" is monosynaptically mediated via the primary endings of the muscle spindles, the Ia fibres, and the smaller "tonic" motoneurones with low thresholds. Not only is the muscle in which the spindles are located activated, but also its synergists are facilitated and its antagonists inhibited. This decerebrate rigidity is often referred to as gamma rigidity. The relative contribution of static and dynamic gamma fibres is not known.

The tendon organs are thought to be active in producing "autogenic inhibition". Activity in Ib fibres is associated with inhibition of the muscle of origin, although it is uncertain how the abrupt onset of inhibition ("clasp-knife reflex") supersedes the maintained excitation caused by activity in the Ia fibres (Matthews, 1972).

The spindle secondaries, besides their role as indicators of muscle length, have been shown to contribute to the tonic reflex tension generated by a muscle (Matthews, 1969; Kanda and Rymer, 1977). Furthermore, Kirkwood and Sears (1974) have demonstrated that a part of this contribution is monosynaptically mediated.

Houk has pointed out that these reflex arcs must serve two requirements which can often conflict (Nichols and Houk, 1976). They must act as a regulator to maintain posture and as a servo-mechanism to execute movements. Clearly, if all muscles possessed an invariable stretch reflex we would be unable to move! This transition from regulator to servomechanism is brought about by central influences on the interneurones and motoneurones.

In man the "gain" of the stretch reflex is normally low, and prolonged tonic responses to stretch are not normally encountered. Granit (1972) has observed that "maintained stretch reflexes fail to occur in man unless the individual is in a pathological state rendering him spastic". Hufschmidt (1966) has compared the tonic stretch reflexes of man with those of the rabbit. He concluded that: "the motor organisation of man shows fundamental differences from those of the animal". Phasic stretch reflexes (tendon jerks) can of course be elicited in most (but certainly not all) individuals. The amplitude of the tendon jerk is open to modulation via the fusimotor system (reinforcement) and by other direct effects on the motoneurone pools. The gain of this reflex is frequently abnormal in pathological states. The muscles of a healthy man can therefore be stretched slowly, without eliciting a contraction, or quickly, in which case a phasic response may be encountered, although this has been questioned by Herman (1970).

Muscle which is being stretched slowly, or which has been denervated, will still exhibit a resistance to stretch which is due to frictional and viscous forces in the muscle itself. Thus the resistance to stretch of a normal muscle is in part a mechanical property of the muscle itself, and in part dictated to it by reflexly induced contraction. If tone is defined as the resistance of a muscle to imposed stretch then it must be remembered that it has a number of components. Pollock (1928) summarised thus: "tension, contractility, elasticity, extensibility, resilience, plasticity, hardness, are all used synonymously with tone. None are tone and all may be a part of it".

The non-neural aspects of tone have been much less extensively investigated than the neural. This is a serious problem, because in investigating for example the stretch reflex, the non-neural changes in tone must be "subtracted" from the overall change in tone in order to determine the contribution of the reflex. Thus Liddell and Sherrington (1924) showed that the stretch reflex produced an extra resistance to muscle lengthening, of extensor muscles in the cat, but inspection of their result (fig. 1.1) shows that fully a quarter of the overall resistance to stretch was contributed by the muscle itself. As this result was obtained in a decerebrate preparation where the stretch reflex gain is

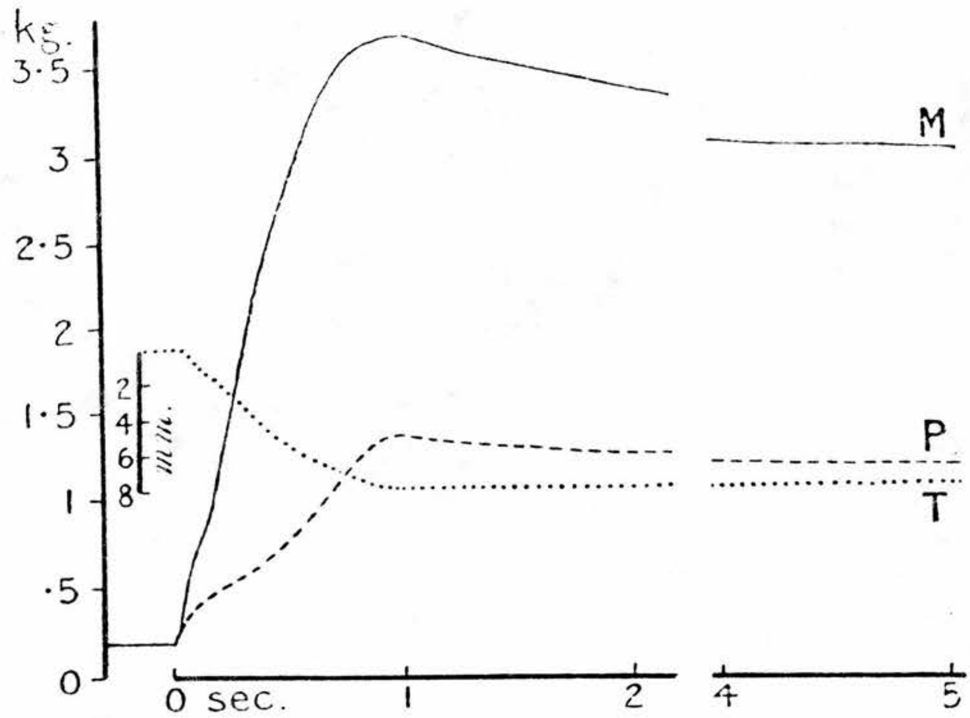

Fig. 1.1 The stretch reflex of Liddell & Sherrington (1924). The muscle of the decerebrate cat is subjected to a length change "T". The tension developed by the innervated muscle in response to stretch is shown by "M", and the tension developed passively by the muscle when its afferent and efferent nerves are severed is shown by "P". The passive tension evidently has a peak value that is more than one third of the reflex tension. In this decerebrated preparation the gain of the stretch reflex is unnaturally high.

artificially high, the relative contribution of the muscle itself under normal conditions might be expected to be much greater.

Denny-Brown (1929) examined the effect of changes of length on an inactive, resting flexor muscle and showed that the response consisted of two phases: an initial stiff response in which the length of the muscle stayed constant and the tension rose rapidly, followed by a region where the tension remained more or less constant as the muscle lengthened. He summarised this by saying that "a muscle, upon being subjected to stretch, at first behaves as an inelastic body and later as an elastic body". The initial stiffness he named "preliminary or stationary rigidity" and he was able to detect this in a muscle at any length where it had been stationary for more than a fraction of a second. The choice of the terms elastic and inelastic is greatly to be regretted; what is really meant is extensible and inextensible. An elastic body is one which will exhibit a completely reversible lengthening in response to an applied force, and Hill (1968) using frog muscles, has shown that the stationary rigidity described by Denny-Brown is highly elastic in nature and he renamed it "the short range elastic component". He also showed that the region of greater compliance had a stiffness that was velocity independent and was thus more characteristic of a frictionally damped, rather than viscously damped, system.

Joyce, Rack and Westbury (1969) and Rack and Westbury (1974) demonstrated an analagous "short range stiffness" in the tetanised cat soleus and lateral gastrocnemius muscles. They also showed that this stiffness is elastic in character. Nichols and Houk (1976) demonstrated similar initially stiff behaviour in unstimulated cat soleus. Grillner (1972) has pointed out that not only must the musculature be able to impose movements, but it must also be able to resist unpredictable externally applied forces, and by making the load compensating mechanism the visco-elastic properties of the muscle itself, inappropriate time lags that occur with feedback control are obviated.

In conclusion, the resistance to passive stretching of a muscle, which is its tone, is dictated in part by factors that are inherent in the muscle itself, and in part by reflex feedback mechanisms which act upon the muscle. The viscoelastic properties that are inherent to the muscle itself may be expected to be a function of the condition of the muscle, its size, temperature, degree of fatigue, etc. The reflex pathways are subject to a wide range of modulating inputs, both directly via the alpha motoneurone pool and indirectly via the fusimotor system. In contrast to the inherent factors which provide an automatic "free" regulation of muscle tone, activity in the reflex systems will change the tonus of the muscle only at the cost of expenditure of metabolic energy by the organism. Influences on reflex control can be either voluntary, involuntary, or most usually, a mixture of both. In measurement of muscle tone one must beware that the procedure employed does not change it, and the large number of factors that contribute to it must be borne in mind.

"There is no clinical method of measuring tone, its estimation depends on impressions obtained by different methods of examination." Gordon Holmes (1952).

1.2) DEVELOPMENTS IN THE MEASUREMENT OF MUSCLE TONE IN MAN

1.2.1) Introduction.

Muscle tone is normally clinically evaluated by the assessment of the resistance encountered when a limb is manually passively moved. Foley (1961) defined tone as the resistance felt by an examiner's hand when passively extending a muscle. This definition is in agreement with the recommendations of the Little Club (1959). This type of manual procedure is liable to human error, the more so as there is a considerable physiological variation in muscle tone. In an attempt to improve on this method, developments have taken place resulting in three quantitative ways of assessing muscle tone.

(1) The measurement of resting electromyographic activity (EMG) based on the principle that increased muscular activity is associated with increased electrical activity.

(2) The measurement of the displacement of a limb produced by a mechanically applied force, or the tension developed by a limb in response to a mechanically applied length change, with or without concomitant EMG analysis.

(3) The analysis of the excitability of the motoneurones by the application of mechanical stimuli (tendon tapping) or electrical stimuli. The mechanical response (muscle jerk) or the EMG activity (H reflex) are assessed.

Method (1) tells us nothing about non-neurally evoked changes in tone, whereas method (2) will distinguish between neural and non-neural components if concomitant EMG analysis is employed. Method (1) assumes that there is a proportional relationship between muscle stiffness and EMG. A relationship of this kind has been demonstrated between integrated EMG and tension developed by a muscle when it is contracting isometrically (Lippold, 1952; Bigland and Lippold, 1954) but it is not certain that this relationship holds under different circumstances (c.f. Moritani and de Vries, 1978). It is a method which possesses several experimental advantages; it is widely used in clinical practice, and it is the only method that is applicable to measurements in conscious unrestrained animals.

In a linear system, the application of force changes or tension changes would be equivalent in method (2), but Roberts (1963) has demonstrated that they are not equivalent in muscle stiffness measurements in the cat, and for consistent results the application of tension changes is to be favoured. Berthoz and Metral (1970) have pointed out that although it is still uncertain whether force is treated as a mechanical variable by the nervous system, the Golgi tendon organs are highly sensitive to force during active contraction, and that at least some of the pyramidal tract neurones in the monkey have an activity which correlates with force rather than position.

Method (3) tells us nothing about the non-neural components of muscle tone, and is really only a test of the phasic sensitivity of the stretch reflex. Its precise relationship to muscle tone is uncertain.

Much of the confusion and uncertainty that has been inherent in the measurement of muscle tone in man has been caused by a failure to appreciate the contribution of neural and non-neural factors, the effects of gravity, and the extent to which application of force or positional changes lead to different results. The claim that it is impossible to measure muscle tone, as the procedure used must alter it, is still sometimes heard.

A very large number of different methods have been employed in attempts to measure muscle tone in man; to quote Smith et al. (1930) : "The problem of the quantitative measurement of the tonus of skeletal muscle in man has been attacked by a number of workers, and by nearly as many methods as workers". This diversity makes it impossible to classify the subject by specific methods. Most of these methods have been ingenious, some are very simple, and others are extremely complicated. To some extent the method employed has been determined by the purpose for which the investigation was carried out; clearly complicated methods employing a room full of equipment may be appropriate for the scientist, but not for the clinician who requires a simple bedside test. As the dividing line between the clinician and the scientist is at best blurred and tenuous, however, no attempt will be made to classify methods of measurement of muscle tone in this way.

The classification that has been chosen deals first with techniques based on category (2) which are direct methods, and secondly with indirect methods which are based on categories (1) and (3).

1.2)2 Direct methods

In the methods to be described here, the muscles are subjected to a change in force or position, and their stiffness or compliance is calculated. These methods are presented more or less chronologically; the later ones which are often combined with EMG analysis, were usually undertaken not so much for measurement of muscle tone as for the evaluation of the properties of the stretch reflex. They are included here because they give valuable information about the neural component of muscle tone.

The early methods of measurement were based on the application of forces to a limb and the analysis of resulting displacements. Early investigators were hampered by the lack of sophisticated force or displacement generating techniques; it is easier to generate constant forces, by means of suitably suspended weights, than it is to generate constant changes in position, although this can be done with a powerful enough motor and an arrangement of cranks and linkages, so most experimenters applied changes in tension rather than length.

Some early investigators (Noyons and Uexhill, 1911; Mangold, 1922; Gildemeister, 1914; and Springer, 1914) constructed machines which give a measurement of the resistance of muscles to transverse pressure on the muscle belly. There is, no doubt, a correlation between the hardness of muscles measured in this way and their ability to resist a stretching pull, but this relationship is not known. Furthermore, considerable error is introduced by the necessity of compressing other, non-muscular, tissues. Such methods therefore found little favour.

The earliest description in the literature of a machine for the specific measurement of muscle tone in man appears to be by Mosso (1896). Mosso, who was professor of physiology at Turin, described an apparatus, a "myotonomètre", which is shown in fig (1.2). The leg is supported in such a way that it hangs vertically

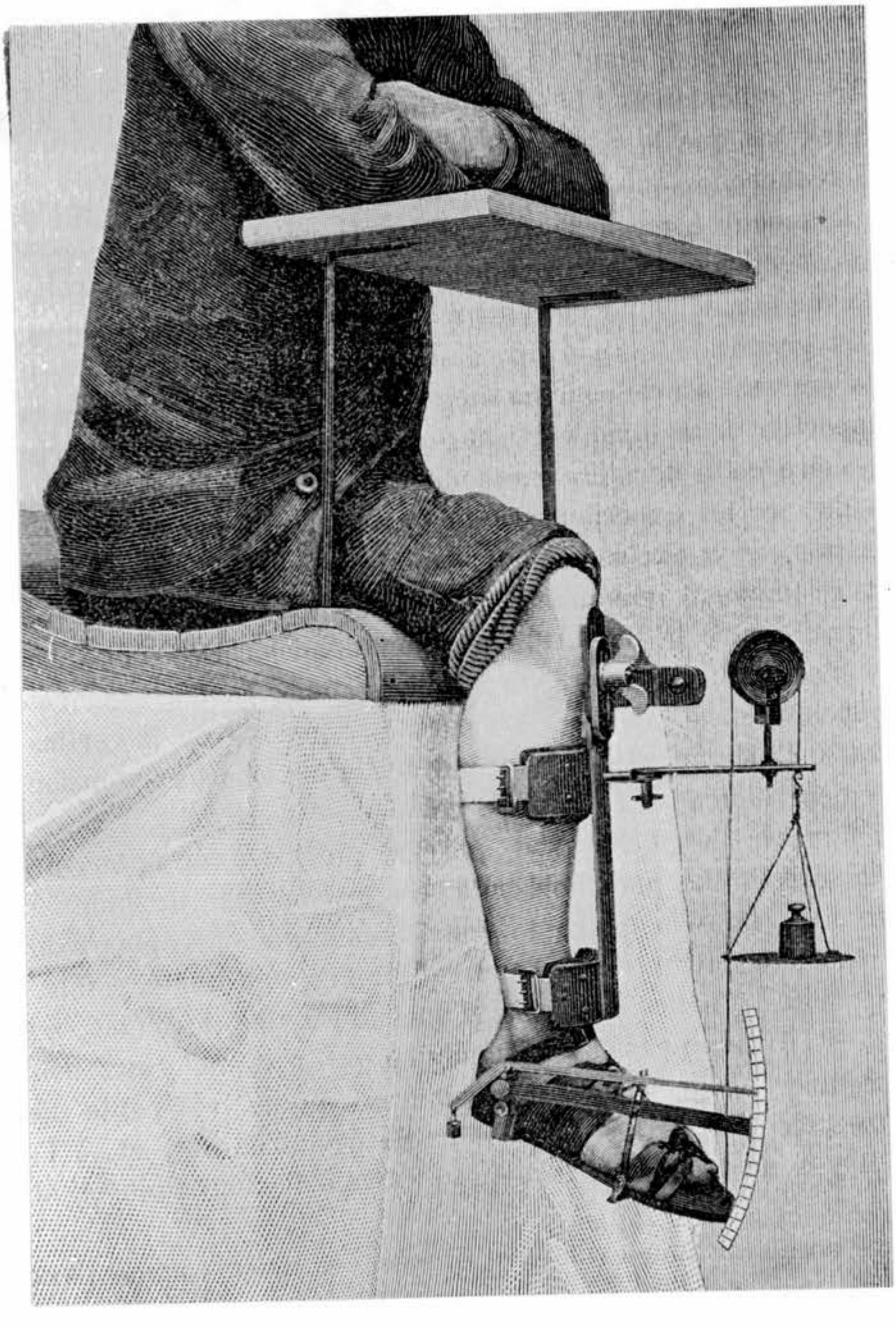

Fig. 1.2 The earliest machine for the measurement of muscle tone in man; the "myotonomètre" of Mosso (1896).

downwards, and forces are applied to the foot by an arrangement of weights and a pulley. Discrete weights, in 100g steps, were added and removed and the angle that the foot adopted measured with the scale provided, or recorded on a smoked drum (not shown). Alternatively, a continuous change in tension could be generated by filling and emptying a vessel with mercury. This is essentially a static method in which the extensibility of the triceps soleus is determined. Mosso, and his collaborator Benedicenti, (1896)* used this apparatus to make a study of muscle elasticity and to investigate the effects of heat and cold, fatigue, and sleep on muscle tone.

Spiegel (1923) and Filimonoff (1925) evolved mechanical techniques for the measurement of the resistance of muscles to longitudinal stretch, and both reviewed the merits and demerits of earlier machines. Many of the methods that they described required data about the moment of inertia, mass, and centre of gravity of the limbs, and this data was usually derived from the work of Braune and Fischer (1890). Braune and Fischer determined these parameters in frozen cadaveric specimens, but their data is scanty, statistically insignificant and therefore not generally applicable (McKinley and Berkwitz, 1928 and Bernstein, 1967).

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* A machine operating on very similar principles had, in fact, been constructed thirty-three years earlier by Donders and van Mansvelt and is illustrated by Hermann (1879). The object of this apparatus, and several which followed it, was not to measure muscle tone, but to study the involuntary overshoot of actively contracting muscles when the load against which they were contracting was suddenly removed. This forms the basis of the "Stewart-Holmes" manoeuvre used in clinical study of movement disorders.

Spiegel (1923) employed a machine,similar to Mosso's, for the quantification of the tone of the knee muscles. The basis of his system was the measurement of the force required to balance the knee at different angles; it was therefore a "static" method. Measurements took place in the vertical plane and the mass of the limb was calculated from the data of Braune and Fischer. This apparatus was used by Kunz and Kerker (1926) in a study of the influence of the sympathetic nerves on muscle tone.

Filimonoff (1925) criticised Spiegel's static system, and employed a system of manually operated spring balances to apply dynamic forces to the knee. The success of this method was largely determined by the skill of the operator, and Filimonoff himself admits that some results were "grossly irregular". The results were comparative, and no attempt was made to express them in units.

Kuznetzov (1925, cited by McKinley and Berkwitz, 1928) employed a clamp mounted on the sesamoid patella to impart forces to the extensor muscles of the knee. He studied the "plasticity" of the muscles; that is, the gradual lengthening of the muscle with the application of a constant force.

McKinley and Berkwitz (1928) appear to have been the first workers to carry out an investigation in the horizontal plane; they employed several machines to investigate different aspects of muscle tone. One of these machines, devised by Dr. L.C. Hutchinson of the University of Minnesota, was driven by an electric motor and this seems to be the first electrically driven machine described in the literature. It may, at one time, have been commercially available. Flexion and extension movements of the forearm were studied. The forearm was driven by an oscillating disc to which it was coupled by a spring. As the spring was relatively weak, the system could operate isometrically or isotonically. Normal male and female subjects were studied, as were patients suffering from hemiplegia, Parkinsonism, and muscular dystrophy.

Pollock and Davis (1932) conducted an investigation into the viscous and frictional resistance to movement of muscles in normal subjects and spastic and Parkinsonian patients. The motorised apparatus employed was that devised by Hutchinson.

Paskind (1932) conducted a series of experiments to investigate the effect of laughter on muscle tone. The apparatus employed was again that devised by Hutchinson. Laughter was produced by means of an anecdote, and in 96% of subjects it was accompanied by a dimunition of muscle tone. Paskind does not say whether jokes can be evaluated by this method; if they can this discovery will surely be seized upon by comedy script writers and the like!

Schaltenbrand (1929) measured muscle tone using dynamometers. The limb under investigation (forearm or leg) was suspended horizontally by leather bands from a hinged metal bar. Forces were applied to the hinged bar by two dynamometers, one for flexing forces and one for extending forces. Displacements of 20-80° were manually applied and the positions and resulting force recorded on a kymograph. This was mechanically more sophisticated than Filimonoff's method, and it operated in the horizontal plane.

Carmichael and Green (1928) analysed the movement of the forearm in patients with Parkinsonian rigidity as it fell through an angle of approximately 80° under the influence of gravity. The apparatus was crude, and only five patients were studied. A similar method was used by Smith et al. (1930) to investigate the muscle tone of the extensors of the knee in normal subjects and Parkinsonian patients. Tone was expressed in Kgf and was the force opposing the displacement. Both these methods relied on the estimates of Braune and Fischer for the moments of inertia of the limbs.

Doshay (1938) described a method for determining the "graphic rigidity index" in Parkinsonian patients. This was done by recording the maximal rate of voluntary contraction of the muscles. The arm, leg, and jaw muscles were analysed. A similar method was employed by Grimmer and Langworthy (1941) in which a method for determining the strength and rate of contraction of wrist and elbow muscles in Parkinsonian patients was described, but no results were mentioned.

Agate, Doshay, and Curtis (1956) and Doshay (1964) devised a complicated apparatus for the assessment of muscle tone in Parkinsonian patients. A motor driven turntable imparted forces to the forearm, and flexion and extension movements occurred in the horizontal plane. The resistive torque was measured by means of a strain gauge assembly. The effect of ethopropazine (parsidol) was investigated and found to decrease rigidity significantly in 50% of cases.

La Joie and Gerston (1952) described an objective method of evaluating muscle tightness. The forearm was strapped to a hinged board and a force was manually applied to cause an angular deflection of 1.5°. The reason for employing such a small displacement is not clear. EMG analysis was also employed. The effect of various physiotherapeutic manoeuvres on spastic muscles was investigated.

Boshes, et al. (1960) and Brumlick and Boshes (1961) have described methods for the study of muscle tone, tremors, movements, and voice in normal subjects and Parkinsonian patients. Their method for muscle tone measurement was based on the resistance encountered by a rapidly oscillating aluminium bar and strain gauge assembly which are coupled to the forearm. Horizontal movements of the forearm occurred over a predetermined arc, and the integrated and averaged resistive torque encountered in a number (usually ten) of swings was calculated. The results of an investigation of thirty normal subjects and thirty Parkinsonian patients were presented.

Webster (1959, 1964, 1966) described an extremely complicated method of measurement of muscle tone by determining the work required to flex and extend the knee. Triangular displacement waveforms (constant velocity ramps) were imposed on the leg, which flexed and extended at the knee in the horizontal plane. The hysteresis loops of torque v. displacement were automatically integrated by a computer, and the work required for a 100^{o} cycle of passive movement was printed out. A wide range of antispastic medication was tested by this method. Difficulties were encountered because of short term and long term fluctuations in the level of spasticity.

Nashold (1966) described a method of muscle tone measurement employing the "Duke" torque recorder. Forces were applied to the forearm by a clutch coupled electric motor and the resistive torque analysed. A similar method, using a less sophisticated "myokinetograph", was described by Martinez (1966).

Wright and Johns (1960) described a method for the measurement of the stiffness of biological tissues. In their method, constant displacements were applied to the body segment under investigation, and the resistive torque analysed. In early experiments the displacement was provided by a pendulum, but this was later replaced by a geared electric motor. Wright and Johns were primarily interested in the rheological properties of joints, but a modified version of their method was employed by Long,Thomas and Crochetiere (1964) who made an elegant analysis of muscle tone in the hand. Their study had two objectives: firstly,to elucidate the nature of normal muscle tone in the hand, and secondly, to investigate the role played by rheological factors in the control of hand movement. The finger under investigation was subjected to constant amplitude perturbations by an apparatus consisting of a geared motor, scotch yoke, and parallelogram linkage. Up to five channels of EMG were simulataneously analysed. This appears to have been the first study in which an attempt was made to distinguish between neurological and mechanical aspects of muscle tone.

In the same year (1964), Leavitt and Beasley imposed tension changes on the muscles of the leg, using hand held electronic "tensiometers" in what was essentially an updated version of Filimonoff's method. Applied torques, knee angle, and raw and integrated EMG were electronically recorded. Movements of the leg took place in the vertical plane.

Timberlake (1964) described a gravity driven ergograph which was designed to apply a constant force to a joint by means of a series of weights, and to record the resultant velocity of movement. In common with all such methods, the problem of variable inertia is encountered; larger weights not only exert a larger force, but also increase the inertia of the system, thus causing ambiguities in the interpretation of a velocity record.

Berthoz and Metral (1970) devised an apparatus which delivered sinusoidal and ramp (trapezoidal) variations in force to the forearm which moved in the vertical plane. A motorised electro-magnetic clutch provided the force. The clutch was controlled by a function generator, and this varied the coupling between the driving plate and the driven plate and so produced torque modulation. As the clutch is rotating in one direction, the system is effectively single acting and it can only serve to vary a continuous pull or push. The disadvantage of this arrangement is that the subject has to exert an opposing force, in order to prevent movement of the forearm. The subject was instructed to maintain the vertical position of the forearm at all times, by referring to a highly damped pointer which was connected to the displacement measuring system. Applied torques were monitored by a strain gauge assembly, and the resulting displacement (which occurred despite the efforts of the subject) was recorded by a potentiometer mounted on the clutch driven plate. EMG recordings were made from the brachio-radialis, biceps, and triceps muscles.

Joyce, Rack and Ross (1974) described a system which was similar in arrangement to that of Berthoz and Metral, but displacement, rather than force, was the controlled variable. A heavy iron flywheel was rotated by an electric drill, and the forearm was rigidly coupled to the flywheel by a connecting-rod and crankpin. The displacement imparted to the arm could be adjusted by altering the position of the crankpin. The reactive force was recorded by a strain gauge bridge mounted at the "little-end" of the connecting rod, and a photoelectric position transducer monitored the displacement of the arm. The flywheel was not driven at a constant speed by the electric drill, but when the desired speed was attained the drive was disconnected. The peak velocity of oscillation of the arm was therefore unpredictable and continuously declining. The entire range of frequencies from 22 Hz down was scanned in less than 30 seconds.

Agarwal and Gottlieb (1977) used a technique which was basically the same as that employed by Rack and his co-workers, except that movements of the ankle were studied and single frequencies could be maintained indefinitely. Dorsiflexion and plantarflexion movements of the foot in the vertical plane were generated by a servo-controlled motor which drove a footplate through a belt. The downward acting force due to gravity was balanced by the upward force of a pair of constant tension springs. The motor provided a steady biasing torque and sinusoidal variations were superimposed on this. The subject exerted a compensatory force in order to maintain the desired position of the footplate. This was facilitated by visual feedback provided by a double beam oscilloscope. Integrated EMG was recorded by disc electrodes over the soleus and anterior tibial muscles.

Herman, Schaumburg and Reiner (1967) described a "rotational joint apparatus" which used a powerful electric motor to drive a footplate via reduction gearing, a silent chain, and an electromagnetic clutch. The arrangement of the apparatus was much as that employed by Agarwal and Gottlieb except that the inputs were in the form of displacement ramps. Dorsiflexion and plantarflexion were studied and ramps of different velocity and amplitude were used. EMG recordings were made using fine wires in the triceps surae and tibialis anterior muscles. Herman (1970) described an investigation of the myotatic activity of spastic muscle using this system; tendon taps were additionally used as an input.

Duggan and McLellan (1973) employed a motorised forearm splint to evaluate muscle tone in the arm. A geared motor drove an eccentric which imposed a sinusoidal oscillation of 13.7° on the forearm. The speed of the motor was controlled by a servo which allowed a range of frequencies to be investigated. The torque was recorded by a strain gauge. Displacement, torque, phase angle between them, and frequency were recorded on a high speed chart recorder. The authors suggested that for routine evaluation of muscle tone the energy absorption at a frequency of 2 Hz and amplitude of 13.7° was a suitable measure. The results obtained using this criterion were compared with conventional clinical assessment for a number of spastic patients and the authors concluded that the correlation was such that the machine could be used for routine clinical measurement of tone.

Marsden, Merton and Morton (1976A) studied the servo-like properties of the flexor pollicus longus muscle. The subject performed a tracking task in which he was required to match the movement of a constant velocity spot on an oscilloscope screen with a spot controlled by the position of the thumb. The movement chosen was flexion of the distal phalanx of the thumb, which was executed purely by the muscle under investigation. Unpredictable perturbations in the force against which the thumb flexed were introduced; these aided or impeded the movement of the thumb.

These forces were generated by a printed armature and their size was measured by a strain gauge. Displacement of the thumb was monitored by a potentiometer coupled to the motor shaft. EMG recordings were made using surface electrodes. "Servo-like responses" were observed; that is, compensatory electrical activity in the muscle which was of too short latency to be voluntary. A modification of this technique was subsequently used to study the servo properties of other muscles (Marsden, Merton and Morton, (1976B)).

A similar approach was employed by Wieneke (1972) who imposed transient torque impulses on the wrist when it was stationary or moving with constant velocity. He was able to show that the impedance of the system is different under these different circumstances.

Hammond (1960) employed an arrangement consisting of a variable speed geared motor which was connected to a flywheel. Drive was taken from the flywheel by a dog clutch and a length of steel tape to the forearm, which was extended from its resting vertical position. This arrangement generated constant velocity stretches after a very brief period of acceleration. Alternatively, a pneumatic piston applied transient force inputs to the system. The applied torque, and resulting displacement, velocity and acceleration were monitored. Suction cup electrodes recorded EMG.

Gurfinkel and his group in Moscow (Gurfinkel, et al., 1975) have studied the contribution of the stretch reflex in the maintenance of a normal standing posture. A motorised tilting platform was employed to impart sinusoidal oscillations to the triceps soleus and ankle angle, antero-posterior sway, and EMG were recorded.

Finally, se veral workers have suggested simple specialised clinical tests for the direct assessment of muscle tone in pathological hypertonia. Wartenburg (1951) described a series of "swing" tests in which upper and lower extremities were manually set into motion and the resulting oscillation examined. These methods have been clinically assessed by Schwab (1963 and 1964). Holt (1963) has described a series of clinical tests, including a pinching of muscles to estimate their hardness, measurements of the range of movement of joints, and estimation of the resistance encountered when muscle is manually stretched.

1.2) 3 Indirect methods

Indirect methods of assessment of muscle tone can be divided into three categories. These are: assessment of electromyographic activity under isometric or isotonic conditions, the analysis of reflex response to mechanical inputs, and the electrical response of the muscle to stimulation of its afferent nerve (H reflex).

Electromyographic analysis was first employed by Piper (1907) and Buchanan (1908). Piper demonstrated that impulses in active muscles arrive with a characteristic frequency of 50 Hz; this was named the Piper rhythm. The recording methods employed by the early investigators were crude and unsatisfactory, the frequency response of the string galvanometers used was poor, and consequently certain frequencies were artificially emphasised; thus the periodicity observed by Piper and others may have been an artefact of the recording system. Technical improvements in the electrodes, and more especially in the recording systems, have lead to electromyography becoming a popular and useful tool for the measurement of muscle tone. It has also been extensively employed in "kinesiology"; the study of the way different muscles contribute to the generation of movements. It is the only satisfactory method of demonstrating activity in a muscle.

Adrian and Bronk (1929) described an improved co-axial recording electrode which they used to study the frequency of discharge in voluntary and reflex movements. This, and later work by Smith (1934) and Lindsley (1935), has demonstrated that the firing of motor units is asynchronous, thus producing a smooth tetanus, and that individual motor units appear to have a maximum discharge frequency of 50 Hz. In a series of three papers Hoefer and Putnam (1939, 1940a and 1940b) investigated the action potentials recorded from the muscles of normal subjects, and from patients suffering from neurological disturbances in muscle tone. They employed a cathode ray oscilloscope and high speed chart recorder and surface electrodes. They were able to demonstrate that in muscle at rest there was no background electrical activity and that this was also true in spastic muscle. This contradicted the earlier work of Gregor and Schilder (1913) and Lindsley (1936). The EMG of muscles in pathological conditions (mainly spasticity) has subsequently been studied by a very large number of investigators.

The relationship between muscular tension and EMG has been studied by Lippold (1952) and Inman, et al. (1952). Lippold was able to demonstrate a linear relationship between isometrically developed force and integrated EMG in large muscles, or in small muscles that do not possess long tendons. Lippold extended his observations to muscles under isotonic conditions (Bigland and Lippold, 1954) and in this work the linear relationship of integrated EMG to muscular tension was confirmed, and a similar relationship was shown between integrated EMG and velocity of contraction. With movements that lengthened the muscle no relationship was found, and thus velocity of lengthening is independent of electrical activity. Burke and his group in Australia have made a detailed investigation of the electrical activity of spastic muscle in response to linear and sinusoidal stretch (Burke et al., 1970, 1971; Ashby and Burke, 1971). Rectified, rather than integrated, EMG was employed to facilitate the determination of the phase of activity and responses were averaged over several cycles to preclude chance variations. Normal subjects, and spastic and Parkinsonian patients, have been studied.

There is now general agreement that EMG analysis demonstrates complete relaxation of resting skeletal muscle (Clemmesen, 1951; Ralston and Libet, 1953). This has been emphasised by Basmajian (1967), and he expresses his views thus:

"In other words, by relaxing a muscle, a normal human being can abolish neuromuscular activity in it. This does not mean that there is no "tone" (or "tonus") in skeletal muscle, as some enthusiasts have claimed. It does mean, however, that the usual definition of "tone" should be modified to state that the general tone of muscle is determined both by the passive elasticity or turgor of muscular (and fibrous) tissues and by the active (though not continuous) contraction of muscle in response to the reaction of the nervous system to stimuli. Thus, at complete rest, a muscle has not lost its tone even though there is no neuromuscular activity in it".

"Straight" EMG is recorded as a series of spikes which vary both in frequency and amplitude. In order to evaluate muscle tone it is therefore necessary to analyse the discontinuous series of spikes, and this can be performed by frequency analysis, or, more commonly, by integration with respect to time. Shaw (1967) has comprehensively reviewed the use of integrators in the quantification of biological signals, and different methods of integration are discussed. In the useful "symposium on skeletal muscle hypertonia" (ed. Levine, 1964) the use of electromyographic analysis in the quantification of muscle hypertonia is discussed by several authors. Tursky reviews several methods of integration of EMG, and EMG analysis is also employed by Levine, Jossman, De Angelis, and Kane who also describe a method for remote monitoring of EMG (telmedography).

The assessment of muscle tone by analysis of the response of the stretch reflex to mechanical perturbations has been employed by a few workers, but with limited success. The obvious problem with this method is the failure to demonstrate a clear relationship between the phasic or tonic properties of the stretch reflex (which is what these methods test), and the degree of muscle tone. There is a substantial group of the population with apparently "normal" muscle tone and a complete or relative absence of elicitable tendon jerks. Similarly, in some pathological hypertonias the stretch reflex may be exaggerated, whereas in others it may be depressed.

Early workers, who had no better methods at their disposal, had perforce to use this method; to quote Mitchell and Lewis (1886): "the responsive jerk brought about by striking a stretched tendon is the most refined measure we possess of deciding as to the tone of a muscle". It is, of course, a method that is still routinely employed in clinical examination of the nervous system.

Jacobson and Carlson (1925) devised an apparatus to measure the height of the knee jerk following a uniform stimulus. The influence of "relaxation" was studied. Erdman and Heather (1964) employed a spring loaded reflex hammer to deliver a constant stimulus to the achilles tendon and the force developed by reflex contraction of the triceps soleus was measured by an optical lever system.

Dietrichson (1973) employed a manually operated reflex hammer containing a force measuring assembly to deliver graded taps to the achilles tendon. The resulting plantar flexion of the foot and the EMG of the triceps soleus were recorded.

A few workers have attempted to assess the neurology of disordered muscle tone by use of the tonic vibration reflex first reported by Granit and Henatsch (1956). A vibration of about 200 Hz applied to the tendon of a muscle brings about a slowly developing slight contraction. This reflex appears to act selectively on the primary endings, and the effects that it produces are very similar to those produced by fusimotor stimulation. In man the response is slow to develop, blocked by anaesthetics, and subject to voluntary control; it is therefore presumably polysynaptic. Hagbarth and Eklund (1966) demonstrated that in decerebrate animals, and in spastic human muscles, the response developed quickly. Burke, et al. (1972) repeated these observations and extended them to cover Parkinsonian patients, who were found to have a slowly developing ("normal") response. It had been hoped by Burke to use this method to distinguish between spasticities of different aetiologies; but this was not possible because of the wide variability of individual response.

The same problem has beset attempts to assess tone by analysis of the H reflex. When a mixed nerve to a muscle is electrically stimulated at an adequate intensity, two electrical waves can be distinguished in the electrical response of the muscle. The first of these is the M wave which is caused by direct stimulation of the motor fibres, and the second H wave (named after Hoffman, 1922) is a monosynaptic response caused by stimulation of large afferent nerves. It is, in effect, an electrically elicited phasic stretch reflex. The amplitude of the H response is, inter alia, a function of the excitability of the motoneurones; and this gave rise to hope that the size of the H response should provide a useful measure of muscle tone. In practice, the threshold of this reflex is so variable that attempts to use it for the assessment of spastic hypertonia have been unsuccessful. Magladery, et al. (1952) were, however, able to demonstrate some inconsistent differences between H reflexes in normal and spastic muscles.

Angel and Hofman (1963) employed the ratio H/M rather than the amplitude of H in an attempt to assess spasticity. This ratio was much higher in spastic muscles but it was so variable that it could not be employed as an index of spasticity.

1.2)4 Concluding remarks

It is often said that where a number of solutions to a problem exist none of them can be satisfactory, and at first sight this might seem to be the case with measurement of muscle tone. It is undeniably true that no method has found universal or even widespread clinical application - there is a school of thought which believes that pathological muscular hypertonicity is best assessed subjectively and that the information obtained is not of much value as it does not relate to anything of which the patient complains. Certainly, most of the methods reviewed here have had as their domain the laboratory rather than the bedside.

However, there are at least two important reasons why the reliable and reproducible measurement of muscle tone is worthwhile.

Firstly, the discovery that certain types of muscular hypertonia are responsive to drugs. It is no coincidence that the two periods of greatest interest in muscle tone measurement were 1920 - 1930 and 1960 - 1970 when the apparently beneficial results of hyoscine and L Dopa respectively on Parkinsonian rigidity had just been discovered. Assessment of any anti-hypertonic spasmolytic drug requires an accurate method of evaluating the results that it produces. The same criterion applies to the treatment of spasticity by pharmacological, surgical, or physiotherapeutic techniques.

Secondly, measurement of muscle tone in normal subjects is an end in itself. A very large part of the central nervous system in man is directly concerned with the innervation of the muscles and the production and control of movement. Clearly, detailed knowledge about the output components of this system can lead to predictions about the design and behaviour of the central elements which are, in man, not readily susceptible to direct investigation. To quote Bevendre (1961): "we can, however, infer certain of the functional properties of the central controlling systems in the brain by a close examination of the output".

This thesis sets out to illustrate factors contributing to normal muscle tone, and to highlight the suitability of a new technique for measurement of muscle tone in normal subjects.

Application of this technique to pathological conditions is also possible.

1.3) THE PRESENT INVESTIGATION

1.3)1 The origin of the technique employed.

The concepts studied are the measurement of muscle tone in man and an investigation of some aspects of the human postural system. A form of transfer function analyser is employed in this investigation - one novelty of this technique is the use of printed armature motors to apply torques to the limb under investigation. This technique was originated by Walsh (1973), who was the first to demonstrate the advantages of this type of force generator in biomedical research. Walsh (1968), too was the first investigator to appreciate the advantages of resonant frequency analysis in studies of the postural system, although other workers, notably Buchthal and Kaiser (1951), Roberts (1963) and Machin and Pringle (1959) had used sinusoidal length and tension changes in the in vivo and in vitro study of isolated muscles.

The application of positive velocity feedback to biological scientific research is also due to Walsh (1975c). One of the many advantages of the printed armature motors employed is that they can rapidly transduce an applied electrical waveform into a corresponding torque output, so great flexibility in the choice of applied torque patterns was possible. Alternative torque waveforms were employed to suit the requirements of the investigation. When a printed motor armature is employed in this type of investigation, two approaches are possible. The motor can be used as a position servo, which will impose a change of position on the limb, or it can be used as a torque servo, which will impose a change of force on the limb.

Roberts (1963) has demonstrated that the changes in length in response to an applied force are more consistent than the changes in tension in response to applied length changes, and consequently the former method was employed in all the experiments to be described. Increased tone therefore manifests itself as a decreased positional change.

2) EXPERIMENTAL

2.1) Experimental Equipment.

2.2) Experimental theory and plan

2.3) Experimental methods

2.4) Experimental errors

2.1) EXPERIMENTAL EQUIPMENT

2.1)1 Introduction.

A photograph of the experimental equipment is shown in fig (2.1) and a schematic block diagram in fig (2.2).

The equipment was designed and built in the Physiology Department, University of Edinburgh. Two sets of apparatus were used in the experiments, but as these are similar only one will be fully described. There are four principal components:- a torque generator, a power amplifier, a waveform generator, and an analyser/recorder.

2.1)2 Torque generator.

The torque generator used in all the experiments is an electric motor of the printed armature type (Printed Motors Ltd., Herts.). A torque generator to be used in this type of investigation must possess the following attributes:

1) Low friction
2) Low inertia
3) Fast and accurate response to command signals
4) Small size

Although, in the past, hydraulic, pneumatic or electromechanical devices have been used in an attempt to meet these requirements, the sophistication of modern electronic engineering has provided a superior solution. The printed motor was developed in France in the early 1950's by the S.E.A. Company. As originally conceived it was to be a low cost d.c. or universal motor which, by virtue of its disc shaped armature, could be mass produced in high volume. Further development demonstrated that the machine possessed properties which made it ideally suited for use as a servo-motor,

Fig. 2.1 The waveform generator/power amplifier/chart recorder unit and the G6M4 motor are seen in use at the wrist.

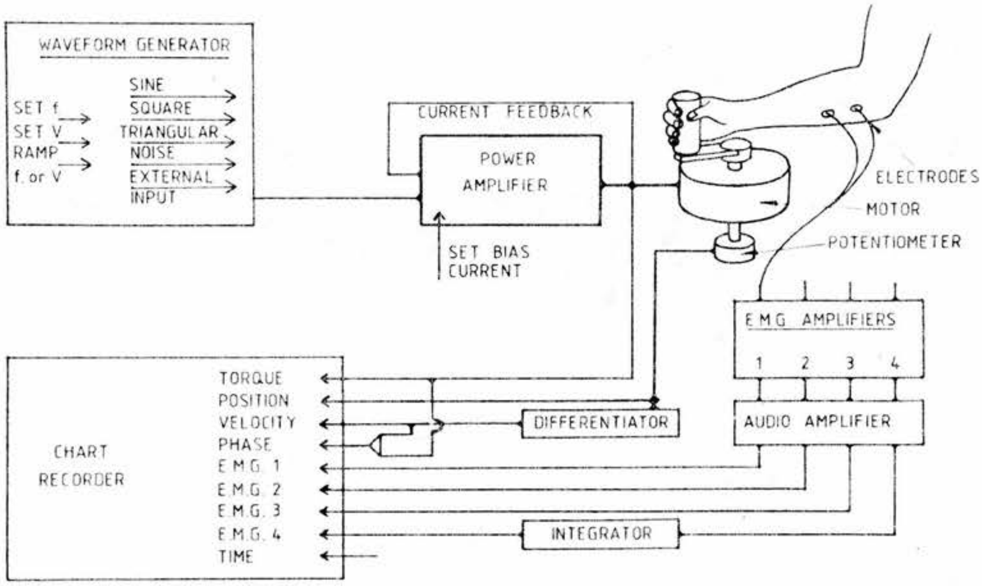


Fig. 2.2 A block diagram of the experimental apparatus.

and it is now to be found in a wide range of sizes and power outputs in applications as diverse as precision data storage systems and electrically powered vehicles. The applications and construction of this type of motor have been discussed by Knight (1975).

In the printed armature, the conventional iron armature is replaced by a circular disc of heat resisting copper coated plastic laminate. The "windings" are etched into the copper surface by a photochemical process. No iron is used in the construction of the armature; because of this there is no magnetic saturation, and the torque output of the motor is linearly related to the current passing through it. This enables the motor's performance to be defined by a number of constants; in servo terms it has a non-varying transfer function. Currents considerably in excess of the continuous limit can be passed through the armature for short periods of time (derating); this permits a very large power to weight ratio. Fast response is assured by the very short, mechanical, and negligible electrical, time constants.

There is no separate commutator as such; the four carbon brushes bear directly on the inner radial ends of the copper windings. The large area of the "commutator" enables a large number of segments to be used (over 100); this eliminates cogging, and ensures a smooth output down to zero speed. As the inductance of the armature is very low due to the lack of iron, arcing at the commutator is not a problem, even when large currents are used commutation is nearly perfect.

The magnetic field is produced by twelve high grade "alnox" magnets arranged above and below the armature with an effective air gap of only 2 mm.

The armature is coupled to a stainless steel shaft, which runs in precision ball-race bearings which are packed with lubricant and fitted with retainers.

The static friction in the motor is due to the bearing surfaces and the axial thrust of the brushes. It is low, typically 55 gcm, and this can be further reduced by modification to the bearings and brushes. The overall inertia of the motor is low and is negligible compared to the inertia of the limb under investigation.

Fig (2.3) is a diagram of the internal components of a printed motor type G6M4. The other motors used in this investigation, G9M4 amd G12M4 are similar, but have an armature diameter of 9 cm and 12 cm respectively rather than 6 cm. The G9M4 and G12M4 motors were used unmodified. However, for some applications it was felt that static friction should be reduced to an absolute minimum, and to achieve this the G6M4 motor was modified. The salient electrical and mechanical data for the G12M4, G9M4 and the G6M4 is summarised in table (2.1)

Details of modifications to G6M4 motor.

The motor was dismantled and the bearings removed. All traces of lubrication were cleaned off the bearings with an organic solvent, and the grease retaining cup-washers, which bore on the shaft of the motor and contributed substantially to friction, were discarded. Two of the four brushes were removed and the tension of the other two was reduced by judicious shortening of their associated springs. We did not reduce the area of the brushes that bears on the commutator (cf. Marsden, Merton and Morton, 1976 A).

Dismantling of the motor and consequent opening of the magnetic circuit caused, as anticipated, considerable demagnetisation.

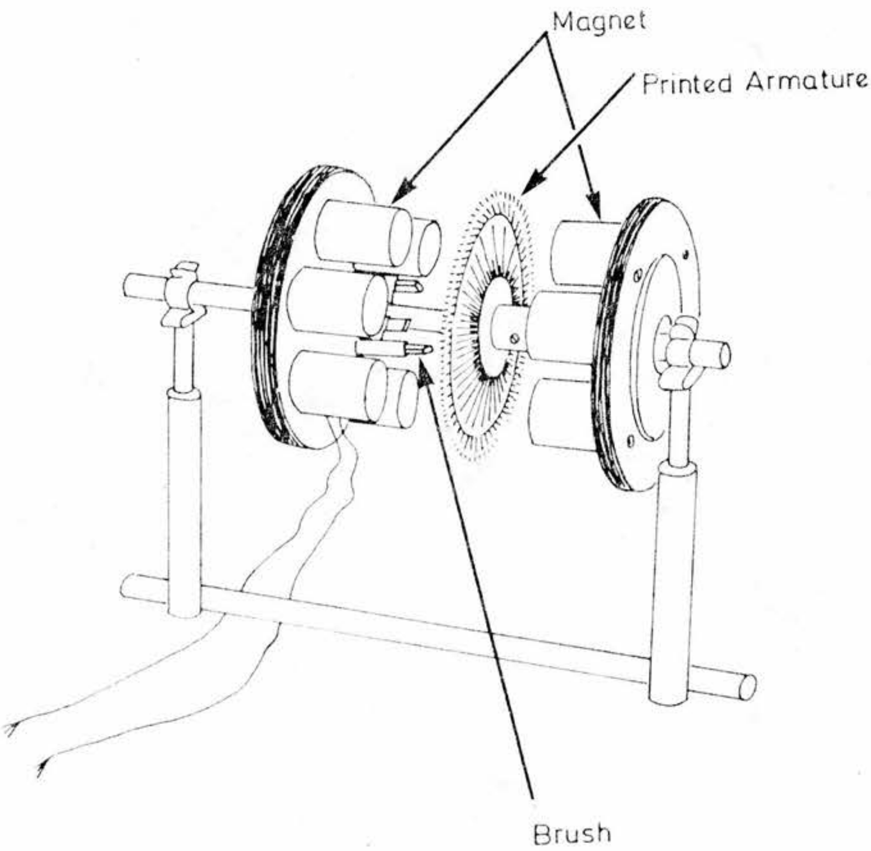


Fig. 2.3 An "exploded" view of the main components of the G6M4 printed armature motor used in the investigations.

Table (2.1) Electrical and Mechanical Motor Constants

Motor	Nominal power (Watts)	Nominal max. torque (continuous) (N m)	Torque constant ($N\ m\ A^{-1}$)	Commutation periods	Inertia ($g.^{*}\ m^2$)	Friction torque (N m)
G12M4	147	0.39	0.080	141	8.0	0.280
G9M4	52	0.18	0.048	117	1.6	0.280
G6M4	25	0.07	0.029	50	0.6	0.052
G6M4 (modified)	25	0.06	0.025	50	0.6	0.015

*The S.I. unit of inertia is Kg m^2, but as this is inconveniently large, g. m^2 (Kg m^2 x 10^{-3}) is used throughout.

Upon reassembly the e.m.f. constant had fallen from 3.1 mv/r.p.m. to 0.6 mv/r.p.m. In the factory, the magnetic field is established by passing a current through heavy gauge wires which are coiled around the magnet. To remagnetise the assembly, a piece of apparatus was constructed consisting of four 400 uf capacitors in parallel and a charge/discharge circuit. The capacitors were charged to 1000 volts and then discharged through the magnet coils by means of a heavy duty switch. This produced a substantial improvement in the e.m.f. constant, 2.7 mv/r.p.m., although this is significantly less than the manufacturer's figure. This, and the fact that one of the pairs of brushes had been removed, meant that care had to be taken not to cause damage to the motor by the application of a large current for long periods of time. It was felt that this small reduction in motor efficiency was an acceptable price to pay for a nearly four-fold reduction in friction. In practice, although forced cooling was not employed, no overheating problems were encountered; this was due to the short duty cycle used.

Mechanical details.

Three torque generators were employed; the G12M4 assembly was practically identical to the G9M4 unit, so only the G9M4 will be described. The G6M4 was rather different and it will be described separately.

G9M4 Unit.

A drawing of this unit is shown in fig (2.4). The motor has a double-ended output shaft, the lower end is attached by a low compliance coupling to the shaft of a precision potentiometer (New England Instruments Inc.), which is mounted on the motor by an

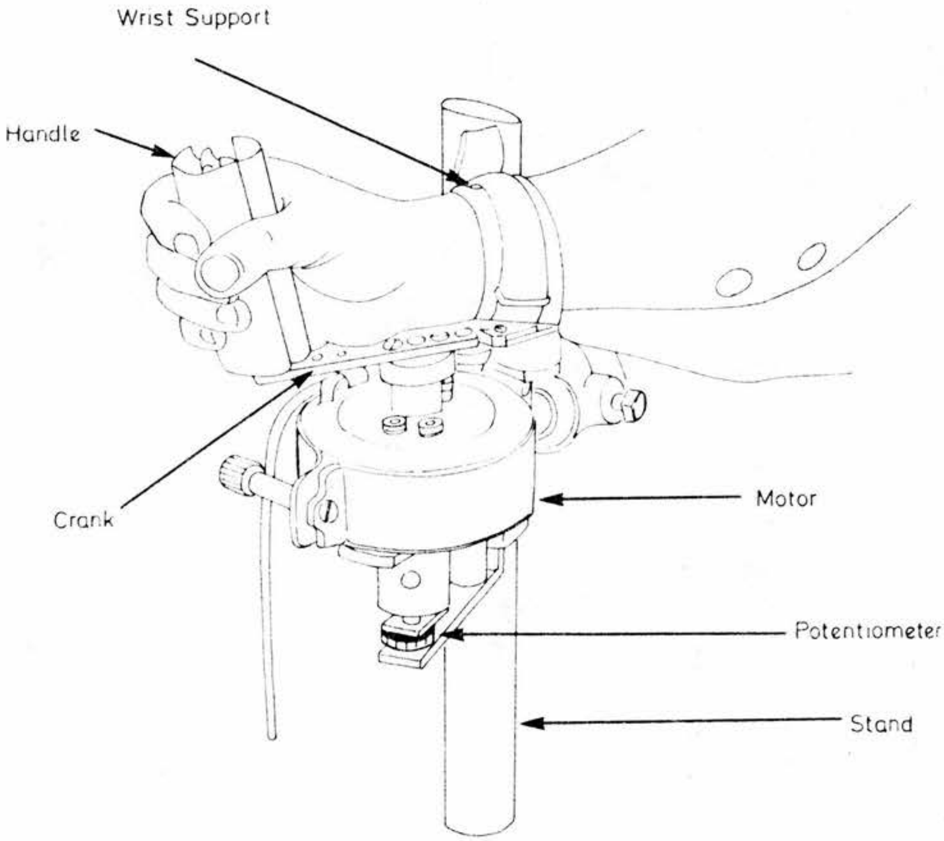


Fig. 2.4 The G9M4 motor is shown in use at the wrist. The arrangement for coupling the limb to the motor is shown, and the site of attachment of the forearm flexor EMG electrodes is indicated.

aluminium plate. The extra friction introduced by the potentiometer and coupling is small, approximately 10 gcm. The coupling incorporates a boss which has a 1 cm hole drilled through it perpendicular to the shaft. Stainless steel "inertia rods" 1 cm in diameter can be inserted into this hole, in order to introduce extra inertia into the system. There are six rods with the following moments of inertia:- 0.5 g. m^2, 1.0 g. m^2, 2.5 g. m^2, 5.0 g. m^2, 20 g. m^2, 50 g. m^2.

The upper end of the motor output shaft is securely keyed to an aluminium boss which has tapped holes in it to permit an appropriate crank to be connected. An aluminium strap passes around the body of the motor, and attaches it to a large tubular clamp by which the assembly is mounted on a suitable stand.

G6M4 Unit.

This unit is smaller than the G9M4 assembly. The motor has a double ended output shaft and, as in the G9M4 assembly, the upper shaft is keyed to an aluminium boss. The boss has a transverse slot into which an appropriate crank can be clamped. There is no coupling to a separate potentiometer in this assembly. The slider of the potentiometer is keyed directly to the lower output shaft and the body of the potentiometer is bonded onto the lower face of the motor. This has the advantage that it eliminates any compliance introduced by the coupling, and does not involve any extra bearing friction or appreciably increase the inertia. Where the shaft emerges from the potentiometer, it has a light boss attached which is drilled to take inertia rods. The upper face of the motor has an alloy plate attached to it which is bolted to a suitable stand.

Potentiometers

The potentiometers used in all three assemblies were 360° precision plastic film types 1 KΩ manufactured by New England Instruments, Inc. At the low currents employed, these potentiometers are free from drift, and have an independent linearity of 0.1%. The starting torque is 10 gcm and the inertia is negligible.

Tachometer

In some of the investigations employing the G6M4 motor, a tachometer (Sperry Gyroscope Co. Ltd.) was used to provide a velocity signal. This gave a signal that was electrically "cleaner" than that obtained by electronic pseudo-differentiation of the position signal, especially at low velocities. The tachometer was attached to the underside of the motor by a tubular sleeve, and their shafts were joined by a low compliance coupling. This introduced a small extra amount of friction and inertia into the system.

A description of how the torque from the motor was conveyed to the limb under investigation is given in the methods section.

2.1)3 Power Amplifier.

The power amplifier is a class B device employing a complimentary pair of power transistors MJ3001/MJ2501. The driving stage of the amplifier incorporates current feedback from the output; this compensates for any changes in terminal resistance of the motor and ensures that the output current is an accurate reflection of the voltage applied by the waveform generator. It thus compensates for the back-e.m.f. of the motor and acts as a torque servo, accurately translating the applied voltage into an output current, regardless of the load externally imposed on the motor. Provision is made for balancing the output stage; normally this is adjusted so that the current through the motor is zero, but,if desired, a constant biasing torque can be arranged.

The maximum output of the amplifier into the motor is approximately 10 amps; this gives a peak torque of 0.3 N m with the G6M4 motor, 0.5 Nm with the G9M4 motor and 0.8 N m with the G12M4 motor. These values of torque are sufficient to produce large deflections of the limbs to which the motor is coupled. The frequency response of the amplifier extends to 100 Hz and is flat down to D.C. In the experiments that were performed the applied frequency did not exceed 50 Hz.

2.1)4 Waveform Generators

The master oscillator is constructed around a 8038BC integrated circuit. It is capable of generating a simultaneous sine, square, and triangular waveform. The output of this integrated circuit is stable and linear in the range 0.001 Hz to 100 KHz. As constructed the oscillator had a frequency range of 0.01 Hz to 30 Hz. The temperature drift of this integrated circuit is only 50 ppm/^{o}C. The frequency of the oscillator is voltage controlled, so it is a relatively simple matter to arrange for its output to be swept over a range of frequencies. In order to do this another integrated circuit is employed as a ramp generator; the size of the sweep obtained and the rate of sweeping can be altered over a wide range. The frequency can be swept upwards or downwards, and the sweep can be linear or logarithmic. It is difficult to sweep the frequency of this oscillator over a very wide range without destroying the symmetry of the waveform at low frequencies. Several circuits have been designed to overcome this problem, and the one that was employed was based on a design by Ainslie (1979).

In the experiments involving compliance measurements, an alternative waveform generator was employed. This uses a ZN425E 8 bit dual mode analogue/digital convertor as a staircase generator. The number of steps can be powers of 2 between 2 and 256 (in the majority of experiments this was set to 32), and the length of the steps can be varied between 0.2 sec and 5 secs. A monophasic or biphasic output can be generated and the staircase can ascend or descend.

In some of the experiments to be described, additional waveforms were derived from a commercial signal generator (Feedback Ltd.).

Fig (2.5) shows the types of waveform used and the constraints that applied to each.

In the positive feedback experiments, a waveform generator was not used; the input to the power amplifier was a signal proportional to the velocity of the motor, and the motor "drove itself". The torque which the motor supplied could be manually controlled, or it could be automatically linearly ramped by a multiplier module (Burr-Brown Ltd.) and a triangular wave generator. A variable offset determined the minimum size of the signal, the height of the triangular wave dictated the maximum signal size, and its frequency controlled the repetition rate.

2.1)5 Analyser/recorder

The analyser and main recorder are built into the same cabinet as the waveform generator and power amplifier.

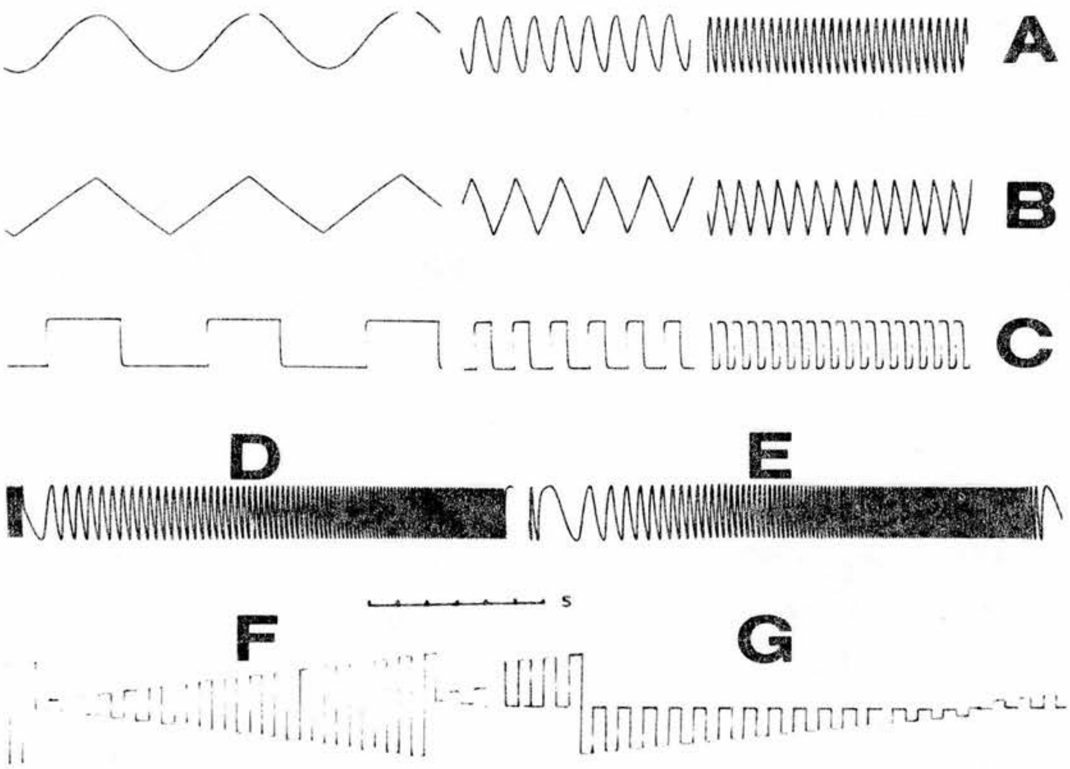


Fig. 2.5 Some typical waveforms:- (A) sine, (B) triangular, and (C) rectangular torques - max frequency 25 Hz, torque 1.0 N m, min frequency 0.1 Hz, torque 0 N m, (D) logarithmically and (E) linearly ramped sinusoidal torque; ramp length adjustable from 0 - 45 s, (F) biphasic rectangular torques, amplitude automatically increasing, and (G) monophasic rectangular torques - amplitude automatically increasing and decreasing - no. of steps 2 - 256, torque 0 - 1.0 N m.

The main recorder is a SLE 8 channel inkwriter type E8b (Specialised Laboratory Equipments Ltd.). The frequency response is 0-150 Hz, down by 6 dB at 150 Hz and flat to 50 Hz. The following functions were routinely recorded.

1) Applied torque. As torque is proportional to current input to the motor, this provides an accurate method of measurement. In practice, the voltage drop along one of the supply leads to the motor is monitored.

2) Displacement. This is recorded by monitoring the voltage developed across the slider of the 360^{o} precision plastic potentiometer coupled to the motor. A bridge circuit is used so that an appropriate base line can be obtained, regardless of the position of the motor shaft. The use of a potentiometer in this way does give a "dead zone" once per rotation, but, as the excursion of the motor never exceeds approximately 150^{o}, the dead zone can be arranged to be outside the recording range.

3) Velocity. This signal is derived from the displacement signal by means of an electronic differentiator circuit based on a low noise integrated circuit. One problem accompanying the use of analogue differentiators is that they are liable to generate electrical noise, and to overcome this problem the frequency response of the circuit must be restricted - in this case to a maximum of 20 Hz. Strictly speaking, the circuit is therefore a pseudo-differentiator. In some of the experiments the velocity signal was generated directly by a tachogenerator (Sperry Gyroscope Co. Ltd.).

4) Phase detector. The phase of the applied torque and the resulting velocity are compared. A triangular waveform of the same

frequency and phase as the driving torque is measured by a sample and hold circuit and measured as the velocity signal goes through zero. The measured value of the triangular wave is therefore displayed twice per cycle. A value of zero implies that torque and velocity are in phase, and indication of whether velocity is lagging or leading torque is provided by a circuit which automatically thickens the trace when the velocity is lagging.

5) EMG. Up to four channels of EMG can be displayed. EMG signals are generally recorded by means of suction cup surface electrodes (Phillips - Bronson type, Specialised Laboratory Equipments Ltd.) but on occasion fine silver wires were inserted into the muscle (details of method in Basmajian and Stecko, 1962). The wires were prepared by removal of the terminal mm of insulation and insertion in a fine (27) gauge hypodermic needle. The assembly was sterilised by autoclaving prior to use. The hypodermic needle was used to position the wires in the muscle under investigation; it was then removed, leaving the wires in the muscle. Different motor units could be recorded by judicious withdrawal of the wires.

The analyser incorporates four EMG amplifiers. They consist of integrated circuit devices, which have a voltage gain of up to 100,000, and a flat frequency response to 1 KHz. Further amplification is provided by the circuits that drive the pen motors. High frequency filtering is effectively provided by the pen motors, which do not respond to frequencies much greater than 150 Hz. In addition, an audio amplifier and loudspeaker, which may be switched to any desired channel, is provided.

A single channel EMG integrator is available; this has a time constant which is switchable between 0.1 sec and infinity. The integrator can also be reset automatically at any desired frequency; this gives a method of comparing the amount of EMG activity in successive epochs.

2.1)6 Other Apparatus

Tape Recorder

Torque and position data could be recorded on a four channel F.M. tape recorder (Racal Thermionic Ltd.). This could be used to replay data of interest at reduced speed onto either the main recorder or one of the others to be described. The linearity of this device is better than 2%, the frequency response at the speed used (7.5 in/s) level to 200 Hz, and the accuracy of reproduction 1%. This apparatus has a low input impedance, so it was always coupled to the main apparatus by means of an isolation amplifier of unity gain and high input impedance. Coded pulses were recorded on a third (spare) channel to aid identification of the record and calibration.

X-Y Plotter

This was employed in conjunction with the tape recorder in most of the compliance experiments. The machine used was a 29000 (Bryans Ltd.). By using the tape recorder, it was possible to drive the X-Y plotter at a suitably low speed; plots of interest could also be superimposed. The linearity of the plotter is 1% for writing speeds not in excess of 0.5 ms^{-1}.

8 Channel Recorder

Some recordings were made with a 8 channel Mingograf ink jet recorder. This has a superior frequency response to the SLE inkwriter (linear to 500 Hz), but the traces obtained are not very suitable for photographic reproduction.

Large Range Recorder

Some compliance measurements were made using a single channel large deflection penwriter (Educational Measurements Ltd.). This instrument is only suitable for recording at low frequencies, as it has a very limited frequency response up to 1 Hz (F.S.D.). It was therefore found unsuitable for recording rapid transients accurately.

Stimulator

A few experiments involved the electrical stimulation of muscle or nerve, using a Devices 2 channel stimulator. The stimulus was applied to the skin overlying the nerve or muscle by means of suction cup electrodes (Phillips - Bronson type, Specialised Laboratory Equipments Ltd.).

2.1)7 Subjects

The subjects who participated in these experiments were volunteers from inside and outside the laboratory. The procedures used were non-invasive and painless; the nature of the experiments was explained to the subjects at the outset. The ages of the subjects ranged from 5 - 78, most were in the 20 - 30 group. Volunteers were of both sexes and widely different body build, fitness, and occupation, although no trained athletes were investigated. Four of the subjects were left-handed.

The subjects who participated in the experiments involving neuromuscular blocking drugs were patients undergoing elective surgery. The appropriate ethical permission was obtained, as was the informed consent of the subjects. The subjects, 11 in number, were of both sexes and different ages and occupations.

Additionally some experiments involved a series of patients who were hemiplegic following stroke.

2.2) EXPERIMENTAL THEORY AND PLAN

2.2)1 Introduction

The investigation of the factors contributing to normal muscle tone involved two types of experimental approach which were based on methods that are routinely employed by engineers and material scientists. Muscle tone has been defined as the longitudinal resistance to stretch of relaxed muscle, accordingly the first type of experiment involved a direct attempt to determine this stiffness.

This method employed the application of forces to the musculo-skeletal system in order to obtain its stress/strain diagram. This technique is very commonly used by material scientists who wish to investigate the properties of a substance, and it has long been employed by physiologists in the study of isolated muscles in vivo and in vitro. As will be shown, this procedure has clear limitations when the substance under examination is appreciably viscous, in which case flow phenomena occur which are velocity and time dependent. As muscle is known to be visco-elastic (Denny-Brown, 1929; Hill, 1951; Buchthal & Kaiser, 1951 and many others), this had to be considered in designing the compliance measuring experiments.

The second experimental approach involved an investigation of the resonance of the musculo-skeletal system. Such a method has two applications in engineering; it is employed in the analysis of control systems and in the investigation of the properties of structures.

When it is used for the study of control systems it is usual to present the information as a vector modulus, or Nyquist plot;

this yields valuable information about the stability of the system at different frequencies, and indicates the useful frequency response of the system. Such techniques have been successfully employed by physiologists to investigate the dynamics of insect fibrillar muscle, which has the ability to oscillate spontaneously when activited and appropriately loaded (Machin & Pringle, 1959).

Simpler analysis is possible when this technique is used to investigate the properties of a material. Resonant frequency analysis can be employed to provide information about the stiffness and mass of structures that are very small in size (for example nuclear magnetic resonance) or very large (for example the analysis of the structures of bridges and aeroplanes). Resonance of the musculo-skeletal system was studied in this way to evaluate its stiffness and mass, and the results were complimentary to those obtained using the more straightforward compliance techniques.

Low amplitude sinusoidal analysis was also used to investigate the non-Newtonian properties of the postural system.

2.2)2 Elasticity, viscosity and visco-elasticity

The compliance of a system is defined as the ratio of the displacement to the applied force. The force versus displacement graph for a perfectly elastic solid is a straight line, the gradient of which is the compliance. This displacement is directly proportional to force; this type of linear behaviour is known as Hookian after its discoverer Robert Hooke who, in 1697, stated "Ut tensis sic vis" - "As the extension, so the force". Although Hooke's law is an approximation, and readily breaks down for large forces, it is of fundamental importance in structural engineering.

The reciprocal of compliance, force/displacement, is also constant in a linear system and this is the Young's modulus of the material, or more simply, its stiffness. Different substances possess different values of Young's modulus, that is, characteristic stiffnesses. This type of elasticity is the familiar property of the rubber band or steel spring.

In the case of fluids a different type of behaviour is found. In a Newtonian fluid, the tension is directly proportional to the velocity of stretching (shearing) and the resulting straight line is the viscosity of the material. Such behaviour is usually modelled by a dashpot, a leaky piston in a fluid-filled cylinder.

A Hookian system requires no net transfer of energy to drive it, energy is stored in the perfectly elastic spring, and is recovered as the spring returns to its resting length. By contrast, a Newtonian fluid is entirely dissipative, it has no ability to store energy, and work must always be performed to displace it.

Many materials demonstrate both of these types of elastic and viscous behaviour in combination, and they are described as visco-elastic. Most biological materials, including skeletal muscle, contain both solid and liquid elements and are therefore visco-elastic.

In many practical materials the elastic resistance to stretching is not that of a linear spring (non-Hookian), and the viscous resistance not directly proportional to velocity (non-Newtonian). Such materials are frequently solutions containing very large molecules, and are usually polymeric materials. Such large molecular protein polymers are frequently encountered in biological systems. Non-linear viscoelastic behaviour is therefore a common property of biological tissues, it has been reported for muscle (Buchthal and Kaiser, 1951), blood (Dintenfass, 1962), skin (Finlay, 1970), and synovial fluid (Davies, 1966).

Such non-Newtonian substances possess a number of properties that distinguish them from Newtonian ones. Their behaviour, which often seems to combine some of the properties of a solid with some of the properties of a liquid, is often spectacular: the classic example is bouncing putty, which can rebound like a rubber ball or flow like treacle. The non-Newtonian properties which are relevant to a study of muscle resistance to stretch include the following:

Shear dependent viscosity

The viscosity of a visco-elastic substance may depend on the velocity with which it is sheared. Frequently the viscosity decreases with rapid stirring and the liquid is said to be pseudoplastic. Most pseudoplastic liquids are also thixotropic, these fluids have a viscosity which is reduced by shearing and the reduced viscosity is maintained for some time after shearing ceases. It is consequently possible to describe a "memory" time for thixotropic substances. The viscosity of a thixotropic substance is therefore dependent on its prior history of movement; Huang and Fabisiak (1976) have pointed out that it is meaningless to give a single value for the viscosity of the blood, as it is a shear rate dependent and time dependent property.

A few non-Newtonian substances exhibit the opposite type of behaviour; they have a viscosity which increases with rate of shearing and they are described as diletant (rheopectic).

Recoil

When some non-Newtonian substances are stretched and immediately released they recoil elastically. Some of these substances can possess a very large amount of recoil, liquid polythene for example, can be stretched to 30 times its original length and will recoil to 3 times its original length, giving a recoil factor of 10, which must be compared to the recoil factor of natural rubber (3), or steel (0.3). If, however, the non-Newtonian substance is held at its extended length, its "memory" fades and recoil is much less complete; viscous flow (creep) has occurred.

Viscous flow

Fig (2.6) illustrates the displacement of a visco-elastic system that is subjected to a rectangular stress. The time course of instantaneous elastic strain (a), slow elastic strain (b) and viscous flow (c) are shown. These give rise to an overall displacement shown in (d). It is noteworthy that the equilibrium position is now different; total recovery does not occur since viscous flow has taken place. This plasticity is an important property of visco-elastic systems; the extent to which it occurs is determined by the nature of the bonds that bind the polymer together. It is not found in polymers that have strong cross linkages.

Stress relaxation

This property is analagous to viscous flow. If a visco-elastic material is stretched, the tension that it exerts declines continuously, in contrast to the constant restoring tension exerted by a rubber band or a steel spring.

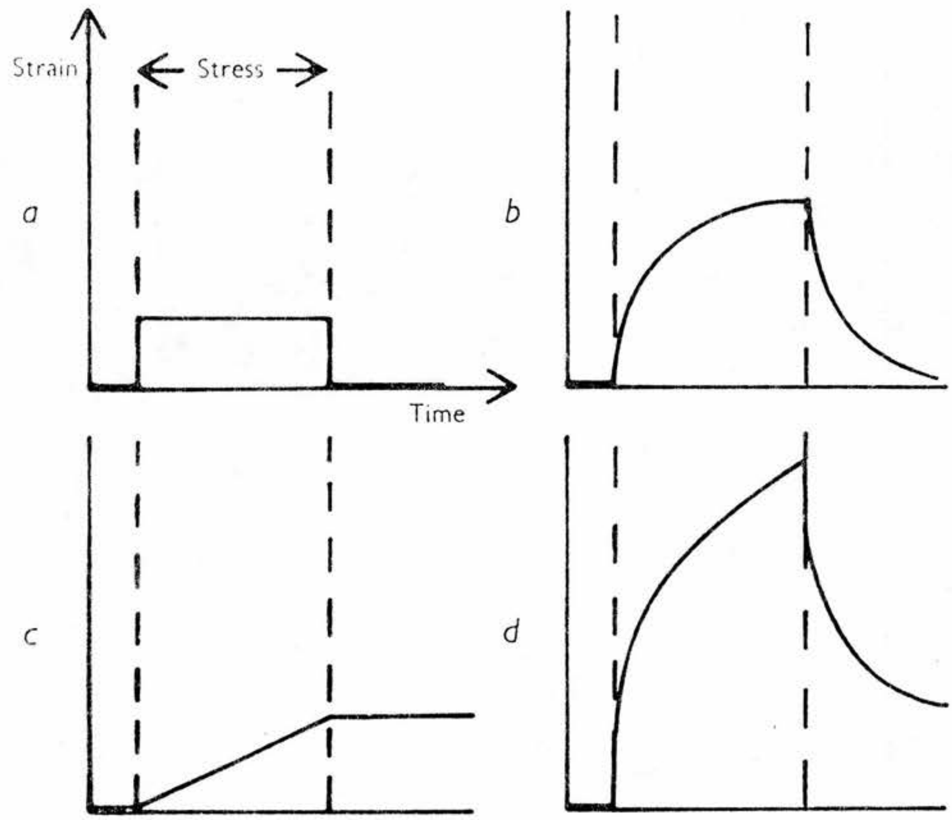


Fig. 2.6 Strain (displacement) of a visco-elastic material in response to a stress (force) applied between the dotted lines: (a) instantaneous elastic strain, (b) slow elastic strain, (c) viscous flow (creep). At (d) the overall response of the material is shown. From Alexander (1968).

2.2)3 Resonance

It is only possible here to provide a very abbreviated introduction to the theory of resonating systems and the problems of sinusoidal analysis; these are treated comprehensively in a number of textbooks (for example Burton, 1968; Thomson, 1964; Feather, 1963). Machin and Pringle (1959) have discussed some biological aspects.

A system which contains a spring and a mass is resonant. The spring resists movement with a force that is directly proportional to its displacement; it therefore resists a sinusoidal displacement with a sinusoidally varying force that is in phase with the displacement, and this force is independent of frequency. The elasticity is measured as the restoring force that the system exerts upon displacement from its equilibrium position, and in a linear system is kx, where x is the displacement and k is the spring constant.

The mass (m) resists changes in velocity; it therefore exerts a force that is maximal as a sinusoidal oscillation reverses in direction, that is, when velocity is zero. This inertial force is therefore also related to the displacement, but it is 180° shifted in phase; it is proportional in size to the frequency of movement squared.

When a system containing both a spring and a mass has imposed upon it a sinusoidal movement, it meets this movement with a force that is a combination of the sinusoidally varying, 180° out of phase, forces due to the spring and mass components. At low frequencies the force due to the mass is small compared to that of the spring, and at high frequencies the force due to the mass outweighs that of the spring. At some intermediate frequency, the resisting force will be zero; the effects of the mass exactly balance the effects of the spring, and the system is at resonance. If the system is perturbed, it will oscillate with a natural frequency that is the same as the resonant frequency.

In any practical system the force exerted by the system at resonance cannot be zero; work must be done to overcome frictional and viscous drag in the system. These forces change in direction as the direction of movement changes, passing through zero as the oscillation halts at either limit; they are therefore of the same phase as the velocity of movement. The frictional force is usually constant in size, whereas the viscous force is usually proportional to velocity (at moderate velocities).

Generally, the mass and spring are treated as separate components of the system, although it is impossible to have a spring with no mass, or a mass that does not act as a spring. As the natural resonance of such a system is a harmonic sinusoidal motion, it is customary to drive the system by means of a similar waveform.

Figure (2.7) shows an idealised plot of the effect of applying a harmonically varying driving force, at different frequencies, to a resonant system. In this figure, the displacement of the system which would result from the same applied statically, is unity on the displacement axis. When the force is instead applied as a sine wave, the displacement becomes dependent on two factors. These are:-

1) The frequency ratio.

2) The damping in the system.

The frequency ratio is the ratio between the frequency of the applied force and the natural frequency of vibration of the system.

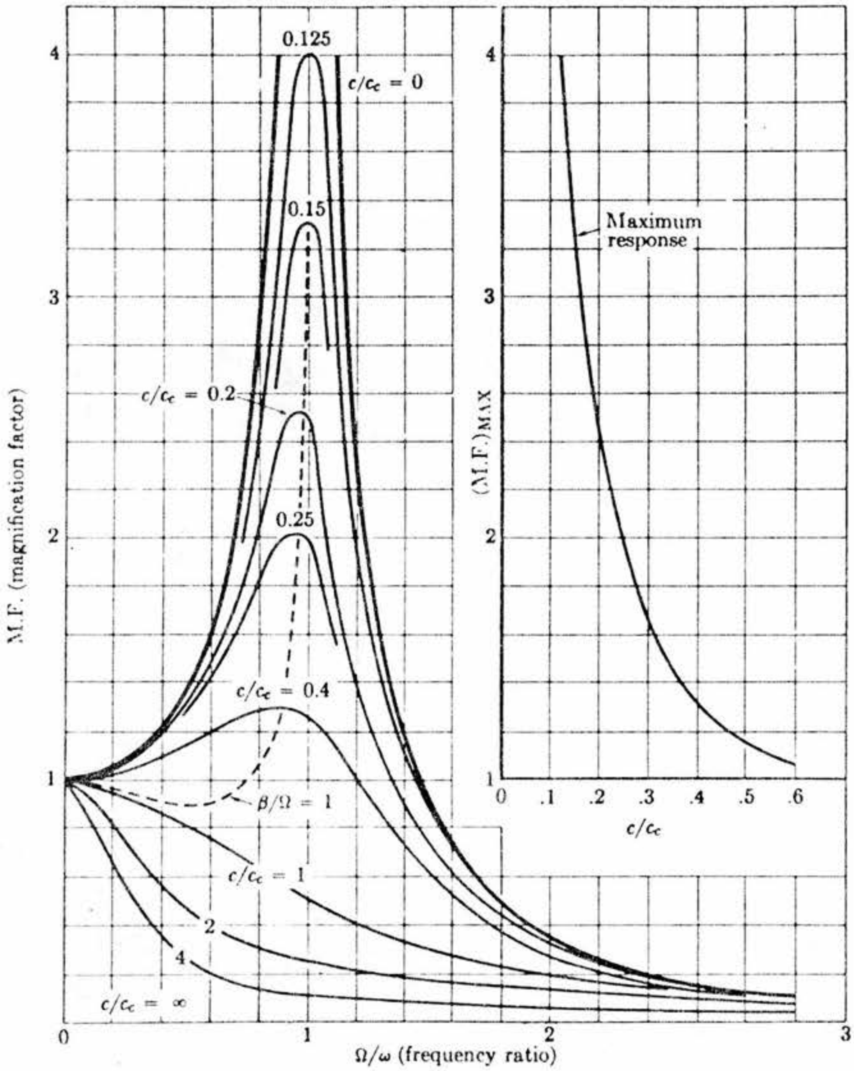


Fig. 2.7 The response of a resonant system at different applied frequencies. The M.F. is the ratio of the deflection produced by the dynamically applied force, to the deflection produced by the statically applied force, and is maximal in a lightly damp ed system when the frequency ratio (ratio of driving force frequency to natural frequency) is 1. A damping coefficient of more than 0.25 effectively distorts this relationship. The relationship of the MF to the damping coefficient is shown in the inset. From Burton (1968).

The damping in the system is caused by frictional and viscous drag. A system that is naturally resonant will not continue to vibrate indefinitely with undiminished energy in response to a perturbation; energy dissipation is brought about by viscous or frictional forces, which cannot be classified as spring or mass effects. The damping in a practical system can have any value from almost zero to virtually infinity.

For any system, a value of damping known as critical damping can be established; this is the value of damping at which the system will cease vibration with least delay following an applied perturbation. For damping = zero, the system will oscillate indefinitely; for damping = infinity it will never return to its resting position.

In fig (2.7) damping (C) has been expressed as a ratio of the damping constant in the system to the calculated critical damping constant (Cc). When C/Cc = 1, there is no peak, and the maximum value of displacement is found when the frequency ratio is zero - that is, for static load applications. When C is less than Cc, the displacement can exceed by several times the displacement that would result from the same force statically applied; when C is greater than Cc the converse is true. It is convenient to define a magnification factor: that is, the ratio between the displacement produced by the force dynamically applied, and the same force statically applied. In fig (2.7) the maximum values of magnification factor are plotted at different values of damping ratio. For a large magnification factor the value of the damping ratio must be low. With zero damping the magnification factor with a frequency ratio of 1 would be infinite. Thus, damping determines the sharpness of tuning, or to borrow a term from electronic engineers, the "Q" of the system.

A very significant feature of fig (2.7) is the way that the point at which resonance occurs varies with the value of the damping. For small amounts of damping the resonant frequency and the driving frequency are identical - that is, the frequency ratio is 1. As the damping is progressively increased, the frequency ratio drifts slightly away from 1 at resonance.

However, in systems that possess low enough damping to show a clear resonance, the disparity is slight. For example, in fig. (2.7) at a damping ratio of 0.4 the system is only very mildly resonant (a magnification factor of only 25% at resonance), yet the error introduced by assuming that the frequency of the driving force at resonance and the natural resonant frequency are the same is only 10%. For lighter damping this error is even less.

Figure (2.8) demonstrates another important property of a resonating system. In this figure the phase angle between driving force and displacement is plotted against the frequency ratio. At a frequency ratio of 1, that is, when the frequency of the applied force is equal to the natural frequency of the system, the angle between force and displacement is invariably 90°. The influence of damping is also shown in this figure, with zero damping there is an abrupt transition from 0° to 180° as resonance occurs, and with progressively greater amounts of damping the transition becomes more gradual.

In a resonating system, the velocity vector leads the displacement vector by 90°, thus at a resonance torque and velocity are aligned, and the phase angle between them is 0°.

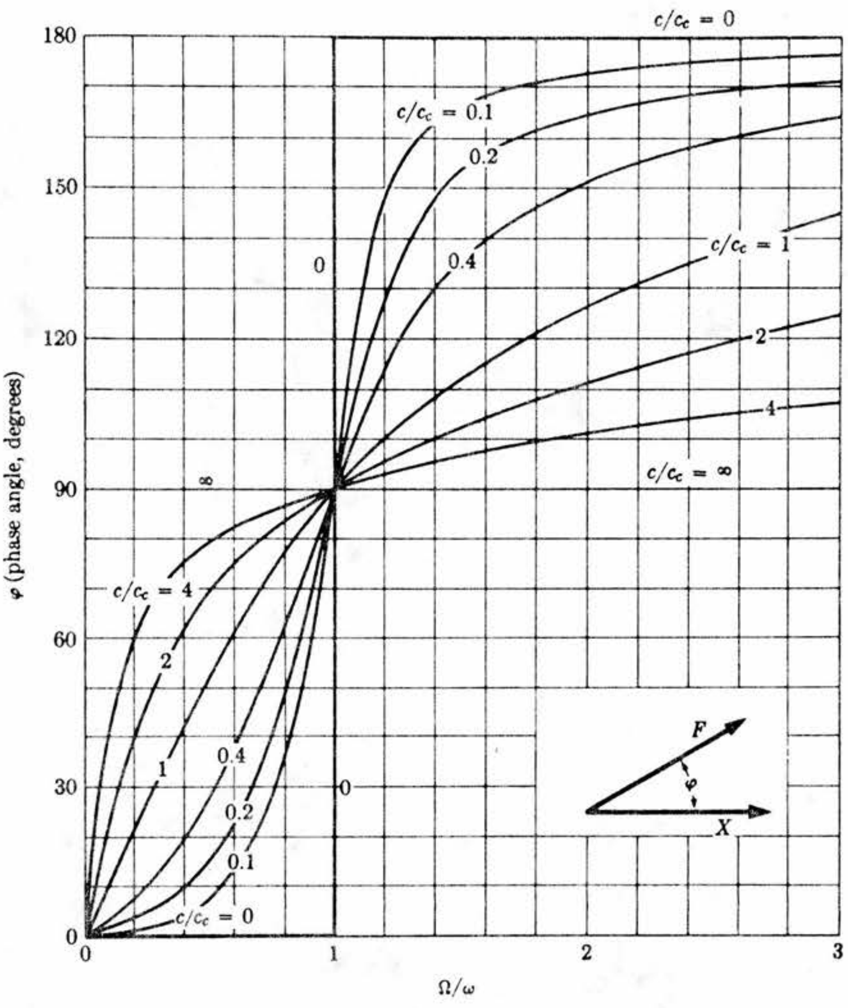
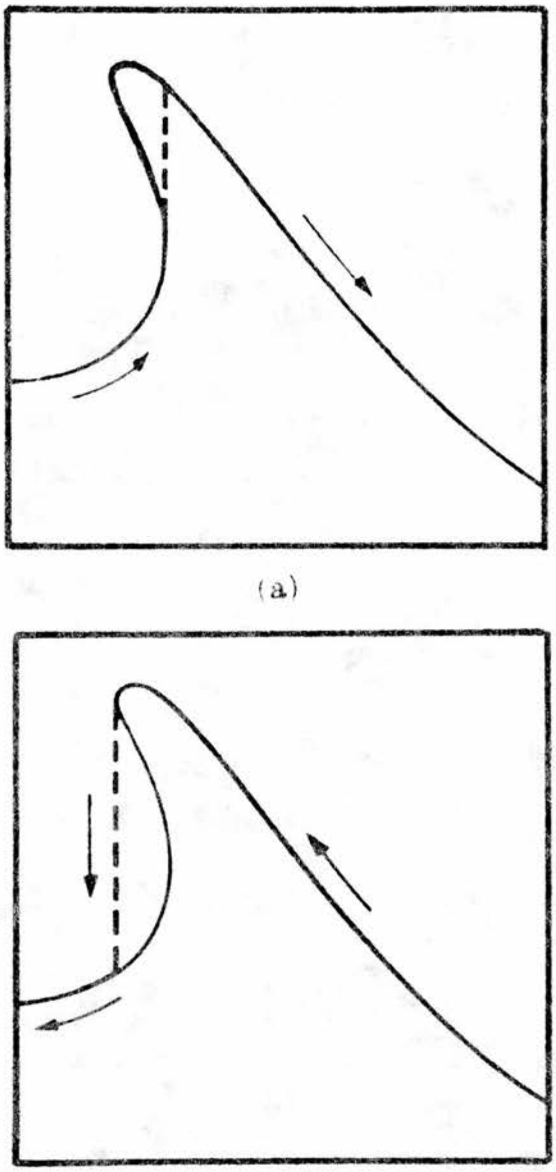


Fig. 2.8 The phase angle between force and displacement. This figure illustrates that, regardless of damping, the phase angle is 90°, when the ratio of driving force frequency to the natural frequency of the system is 1, i.e. at resonance. As the velocity vector leads the displacement vector by 90°, the phase angle between torque and velocity at resonance is 0°. From Burton (1968).

In a linear undamped system, where k is non-varying, the resonant frequency is dependent only on the values of k and m. Non-linear springs exist where the value of k is not a constant but is related to the value of x; in such cases the amplitude of the vibration has an effect on the resonant frequency. This type of non-linearity can have two forms - the value of k can increase with displacement, in which case the spring is said to be a hardening spring (an example of this is the cart spring where increasing deflection progressively involves more leaves), or the value of k can decrease with deflection in which case it is described as a softening spring (an example of a softening spring is a pendulum system, where the restoring force is not proportional to the angle of displacement (Θ) but to sin Θ; as Θ increases the value of sin Θ, becomes progressively less than Θ).

The effect of a non-linear value of k on the resonance of a system is predictable. A system comprising a hardening spring will have a higher resonant frequency for large displacements than small ones, and with a softening spring the converse will be true. Figure (2.9) illustrates the relationship between the displacement of a softening spring system, and the ratio of the driving force frequency to the natural frequency (cf. fig (2.7)). Figure (2.9) also shows a peculiar type of irreversibility for increasing and decreasing frequencies. For this lightly damped softening spring system, as the frequency is increased from zero the response follows the lower curve until this curve turns back to the left. It then abruptly joins the upper-most curve. If the frequency is now decreased, the response will follow the upper curve until this curve reverses direction, whereupon it abruptly rejoins the lower



(a)

(b)

Fig. 2.9 The response of a non-linear softening spring system as the frequency of the driving waveform is (a) increased and (b) decreased. The theoretically predicted response is shown by the solid line, but as the driving frequency (abscissa) is changed, the response (ordinate) "jumps" upward or downwards (dotted line). The size of the response is therefore unstable and unpredictable over a certain band of frequencies.

curve. This abrupt transition has been called a "jump" effect. It is evident that a softening spring system can be brought up to frequency without reaching its maximum response, but it does reach the maximum response upon decrease of frequency from a high value. The hardening spring system responds in exactly the reverse manner. Thus, at certain frequencies, in a non-linear system it is possible to have very different amplitudes, depending on whether the system has been subjected to an increasing frequency, or a decreasing frequency.

A system that combines viscous damping with elasticity will be visco-elastic; the properties of such systems have been discussed in the previous section. It is of course possible for the viscous damping to be non-linear - thus the system may be pseudoplastic, thixotropic or diletant.

It is also possible for a system to have a non-linear mass (an example of this is the Catherine Wheel, in which the mass constantly declines).

Systems that contain non-linear elements do not oscillate with a simple harmonic motion, and Fourier analysis, or other methods based on the superposition of solutions, cannot be used. Because of this, it is usual to treat such systens in a linear way and to accept that the solution is an approximation (Burton, 1968). This is particularly applicable to biological tissues, many of which are known to be highly non-linear. However, it must be remembered that:

> "Under these circumstances information obtained during sinusoidal movement at one amplitude does not necessarily predict the behaviour of the system with other amplitudes of movement, and simple linear transfer functions are of very limited value since they describe the behaviour of the system only under the conditions in which they were measured." (Joyce, Rack and Ross, 1974).

To demonstrate these non-linearities, sinusoidal analysis was performed using a wide range of driving torque.

2.2)4 Experimental plan

The experiments involving sinusoidal analysis were designed to ascertain the stiffness (tone) of the musculo-skeletal system and to investigate the non-linear properties of this system.

The approach employed was straightforward; the limbs were mechanically oscillated with sinusoidally varying torques, and the driving system and attached limb treated as a torsional pendulum. This permitted the calculation of the stiffness of the limb, and also incidentally of its moment of inertia. The conventional engineering technique of sweeping the driving torque exponentially through the desired range of frequencies was employed, and many different levels of torque were used to investigate non-linearities. The resonant frequency was identified by establishing the frequency for which the magnification factor was maximal, and confirmed by an analysis of the phase angle between torque and displacement waveforms.

The experiments to determine the compliance of the musculo-skeletal systems were designed to further investigate the non-linearities of the system and to study its visco-elastic properties. In the study of visco-elastic systems, a standard approach is to apply known values of force to the system, and to analyse the resulting displacement and velocity components. This is the approach that was employed in the analysis of postural tone. Rectangular torque pulses were applied to the limb under test and the resulting displacement and velocity recorded, yielding information about the elasticity and viscosity respectively. Different sizes of torque input were employed to obtain information about non-linearities in the system.

Some of these non-linear visco-elastic properties were also studied by low-amplitude sinusoidal analysis.

The effects on wrist muscle tone of cooling the muscles of the fore-arm were investigated using all three of these methods.

In all the experiments undertaken, concomitant EMG analysis was frequently employed to investigate the extent of neural contribution to postural tone. Trial experiments were carried out to establish suitable values for driving torques and frequencies etc. The emphasis in all the experiments was not placed on obtaining a detailed numerical statement of "normal" values of muscle tone for different body segments, rather it was directed to obtaining a broad overview of muscle tone and the investigation of a new technique suited to its measurement.

2.3) EXPERIMENTAL METHODS

2.3)1 Introduction

The aim of all the experiments undertaken was the study of the resistance of relaxed muscle to passive stretch (muscle tone) in man. Such investigations are difficult for the following reasons:-

1) Muscles in man are not accessible and, apart from trivial cases, movement of muscles must involve movement of a joint. Thus it is impossible to separate the components of resistance into those caused by muscle and those caused by the joints themselves.

2) It is generally impossible passively to move one muscle without causing movement of muscles that are synergistic or antagonistic about it. In effect, this means that muscles must be investigated in groups rather than individually.

3) Muscles are under voluntary and involuntary nervous control. Care must be taken that the procedure adopted to investigate muscle tone does not itself alter it by eliciting short or long loop reflex activity.

At first sight these constraints may appear to be disadvantages: however it is often an advantage to study the behaviour of an entire system rather than its component parts. In this case it is hoped that doing so will bridge the gap between muscle physiology and the mechanics of postural stability. There is, after all, much evidence to suggest that patterns of movement are controlled, rather than the activity of single muscles. Certainly, what is being studied is muscle tone as a physician understands it.

2.3)2 Methods: general

The experiments were performed in a quiet warm room (20^{o}C). The experiments involving neuromuscular blockade were carried out in the anaesthetic room of a hospital. Care was taken to ensure that the subjects were as relaxed as possible. Any records obtained while the subjects were disturbed or distracted were rejected. Often naive subjects were found to become more relaxed during the first few minutes of experimentation. Their compliance would increase and their tonic EMG would decrease to a low level (usually zero). This effect was not seen with experienced subjects. Measurements made during the first few minutes of recording were not used. Occasionally a subject was encountered who was unable to relax; these subjects were not used in the study.

Subjects were seated in a comfortable chair, or, in the case of the neuromuscular blockade experiments, were recumbent. Experimental sessions were generally limited to a maximum of about 30 minutes as it was felt that physical or mental fatigue might affect the results. The procedures were not painful or stressful, indeed subjects were sometimes found to doze. Great care was taken to ensure that the axis of the joint under investigation was concentric with the shaft of the motor, and frequent checks were made to ensure that it remained so.

2.3)3 Measurements at the wrist

These formed the great bulk of the experiments. The G9M4 and G6M4 motors were used at the wrist. Subjects sat in a comfortable chair and the arm under investigation was supported by a stand. The position used was with the upper arm pointing downwards, and the elbow flexed at 120^{o} pointing forward. The wrist was firmly attached to a padded support by velcro strapping and the fingers grasped the handle, which was attached to the output crank of the motor. The handle was hollow and a light velcro strap passed through it and held the fingers against it. No effort of will was required to maintain the position of the wrist and hand; this was shown conclusively by the experiments on anaesthetized subjects.

The supporting structure could be adjusted to suit subjects of any build and the throw of the crank could be adjusted so that the wrist joint was properly concentric with the axis of the motor. Particular attention was paid to this point. It was desirable to exclude the effects of gravity; accordingly motion took place in the horizontal plane and the apparatus was carefully levelled. The stands used were of heavy construction in order to eliminate any troublesome resonances in them; even so there was a slight resonance at about 45 Hz - this was however well outside the range of frequencies in which we were interested. The movement studied was flexion and extension of the wrist.

The position of the motor and supporting system could easily be changed from the left side of the subject to the right side, and in the majority of cases both wrists were investigated consecutively. At times, however, it was more convenient to analyse a small "batch" of, say, three left wrists followed by three right wrists. Some subjects were investigated on only one side. Many subjects were tested on more than one occasion to assess the reproducibility of the results.

2.3)4 Measurements at the elbow

The G9M4 and G12M4 motors were used. The same apparatus was employed as in the wrist investigations, but the method of attaching the limb to the motor differed. The subject sat in a comfortable chair. The upper arm was abducted and the forearm rested in a cradle attached to the motor crank. The shaft of the motor was concentric with the elbow joint. The hand was pronated and supported with a shaped polyether foam block. The forearm was retained in the cradle by means of light elastic bandaging. Because the forearm has considerable mass, great care was taken to ensure that the apparatus was levelled and that the flexion/extension movements occurred only in the horizontal plane. Twenty-three subjects were studied but only nine were analysed on each side. Several subjects were investigated on more than one occasion.

2.3)5 Measurements at the knee

The G9M4 and G12M4 motors were used. In these experiments the subject lay on one side on a couch. The leg that was uppermost was supported by a splint and sling attached to the motor output crank. The motor was supported coaxially above the knee joint by means of a heavy metal stand. Six subjects had a knee tested. As in the other investigations, considerable care was taken to ensure that the motor shaft was concentric with the joint and that the flexion extension movements occurred in a horizontal plane.

2.3)6 Measurements at the ankle

A similar system to that used for the knee was employed, but a specially constructed foot-plate incorporating ball-race bearings was used to convey the force from the motor to the limb. The subject lay on one side and the ankle that was uppermost was analysed.

The leg was supported with shaped plastic foam blocks. Ten ankles were investigated.

2.3)7 Measurements at the finger/jaw

These investigations differed from the previously described ones because the motor could not be directly coupled to the limb. To convey the force of the motor to the limb, a light linkage was employed. To minimise friction, all joints were constructed of stainless steel pins located in PTFE bushes.

The finger was driven by a light linkage which was coupled to a small plastic plate bandaged to the finger nail. The hand was supported by a specially shaped wooden block. The proximal and distal phalanges of the ring or index fingers were studied. Flexion and extension movements occurred in the horizontal plane. The axis of the motor (G6M4) was concentric with the joint undergoing investigation. Inevitably some movement took place at the distal joint when the proximal joint was being studied. Five fingers were investigated.

Only one experiment was carried out on the jaw. The subject lay supine and the force of the motor was conveyed to the mandible by means of a light rod and crank. A secure clamp, incorporating a balsa wood bite, attached the system to the jaw. The motor was not concentric with the jaw, and since the jaw was moving in a vertical plane gravity could not be eliminated. The head was supported by a shaped plastic block which was rigidly mounted on a heavy baseboard. Despite this, there was some oscillation of the head and neck. Elevation and depression movements of the jaw were studied.

2.3)8 Measurements in anaesthetised patients

These experiments were conducted in the anaesthetic room of a hospital operating theatre. The patients selected for study were candidates for elective surgery. Five patients had prolapsed intervertebral discs which necessitated laminectomy; the remainder were receiving abdominal surgery. The informed consent of all patients was obtained before the investigation was undertaken. The experiments were conducted continuously, before, during, and following anaesthesia. The patient lay supine on a hospital trolley and the wrist and forearm were attached to the apparatus. A special stand was constructed for this purpose. In some cases EMG recordings were made. All subjects had the left wrist analysed as the anaesthetist preferred to work on the right side.

The investigation was started about fifteen minutes before anaesthesia. Anaesthesia was induced by barbiturate and maintained after intubation by halothane or nitrous oxide/oxygen. Before intubation, neuromuscular blocking drugs of the competitive or depolarizing type were administered intravenously. Further doses of blocking drugs were administered subsequently, prior to removal of the patient to the operating theatre. At least ten minutes of recording time was available after anaesthesia. An event marker was used to indicate on the record the times at which drugs were administered, and other procedures carried out. Only wrists were investigated in anaesthetised subjects.

A portable clinical stimulator was used to establish the extent of the neuromuscular blockade in some cases; but all patients ceased spontaneous respiration, and had to be artificially ventilated.

2.3)9 Cooling experiments

These experiments were carried out only at the wrist. Two methods of cooling were employed.

The first cooling experiments involved a simple immersion technique. A control measurement was made at the subject's wrist, and the subject then immersed either the entire forearm or the hand and wrist only into a tank of water at about 7°C for a period of five to fifteen minutes. The subject then withdrew his arm from the water, dried it, and the measuring apparatus was reconnected. The disadvantages of this method were:-

1) It is not possible to record continuously as the subject is cooled.

2) By the time that the apparatus is reconnected, rewarming has started.

3) EMG recordings were not practical.

In an attempt to overcome these problems, a special piece of apparatus was constructed. The forearm was enclosed in a metal tank which had a hole in one end through which the wrist was passed. The wrist was supported by preformed plastic foam, and a watertight seal was provided by a modified surgical nylon glove. Water was pumped continuously through the tank from a larger container, where the water temperature was thermostatically controlled. The minimum water temperature achieved was about 2°C. Control measurements were made at a temperature of 35 $\pm$ 1°C. The rate of flow was sufficient to ensure that the contents of the tank surrounding the forearm were well stirred.

Skin temperatures were recorded by means of a twelve channel telethermometer and disc thermistors. On four occasions, EMGs were recorded using fine silver wire implanted in the muscles. Problems were initially encountered with immersed suction cup electrodes, but when a very high impedance EMG pre-amplifier was substituted for the one in use, these difficulties disappeared, and underwater EMG recordings were routinely made in this way.

Immersion of the forearm in cold water lasted for thirty to sixty minutes; this was judged to be long enough to cool the muscles and other deep tissues. As immersion of the arm in water at this temperature is initially painful, subjects were instructed to terminate the experiment whenever they wished.

2.3)10 EMG recording

In many of the investigations EMG recordings were made. Generally, surface EMGs were recorded using suction electrodes (Philips-Bronson Type, Specialized Laboratory Equipment Ltd.) and electrode jelly (Cambridge Ltd.). The electrodes were chlorided from time to time in accordance with the manufacturer's directions. The skin was microabraded and degreased using alcohol before attachment of the electrodes. Placement of electrodes follows the scheme suggested by Davis (1952). On some occasions, fine (50 micron) silver wires (Johnson Mathey Ltd.) were used to provide recordings of individual motor units or small numbers of motor units. These wires were inserted into the belly of the muscle by a hypodermic needle. By judicious pulling on the wires, their position in the muscle could be altered. It was often possible to record the activity of single units, which were identified by monitoring the spikes on an oscilloscope screen.

2.4) EXPERIMENTAL ERRORS

2.4)1 Introduction

The results were calculated when the experiments were completed. The data was in the form of ink traces on recording paper. The paper speed was generally 7.5 mm/sec; higher speeds were used when it was desired to study transients or measure time intervals with greater then normal accuracy. The average length of a recording for an experimental session was about 20 metres.

All measurements on the recording paper were performed manually using a x 8 magnifier with an integral illuminated graticule. The data from each recording session was tabulated. Most of the calculations that were performed were simple and were performed manually. However, to simplify the large mass of observations in the wrist resonant frequency experiments, and to check on their statistical significance, a computer was used.

2.4)2 Sources of error

There are many sources of error in measuring analogue, non-quantal signals using a chart recorder. These are:-

a) Observer error (both interobserver and intraobserver).

b) Inaccuracies and non-linearities in the recording system itself, i.e. the pen motor, pen assembly (arc distortion), chart drive, paper shrinkage, etc.

c) Inaccuracies and non-linearities in the electronic processing of analogue signals, i.e. in the amplifier system.

d) Inaccuracies and non-linearities in the transducers that provide the analogue signals, i.e. the potentiometers and tachometers.

e) Inaccuracies in circuits that provide timing signals.

This wide range of possible sources of error and the fact that many of them were dependent on parameters such as amplifier gain and recording speed made it unrealistic to calculate errors. To evaluate the accuracy of the system and to calibrate it, simple empirical techniques had to be employed.

2.4)3 Calibration and measurement of errors

Torque

The torque provided by the motors was directly proportional to the current passing through the armature. The manufacturer's specification provided a value for this torque constant for each motor. However, the G6M4 motor, which was modified to minimise friction, was partially demagnetised and its torque constant was therefore lowered. Also, the relationship between torque and current does not hold at extremely low levels as a certain current is required to overcome the static friction of the motor before any useful external torque is developed.

Accordingly, all the motors were calibrated in conjunction with the recording system. A lever of known length was connected to the motor output shaft. The end of the lever bore, via a knife edge, on the scale pan of a precision electronic laboratory balance. The current through the motor was monitored by a sensitive ammeter. A calibration curve of torque v. current could thus be plotted for each motor. As anticipated, this yielded a straight line which did not pass through the origin. The deflection of the recording pen produced by currents of up to 10A (the maximum current used in practice) was noted, and the overall resolution of the system was calculated at 2%.

The error was largely caused by measuring difficulties due to the thickness of the lines. This level of accuracy could be improved on by using higher gain at the recorder, but this meant that the maximum torque that could be recorded was correspondingly reduced.

Displacement

A circular protractor was positioned with the motor at its centre, and a fine pointer was attached to the output shaft. The motor and potentiometer assembly were then manually rotated by one degree increments. The largest excursions of the motor encountered in practice were about 120° (2.0 rad). If the recording gain was set so that the f.s.d. of the recorder was equal to 120°, the resolution was 2° (0.03 rad). When smaller movements were being recorded the chart recorder gain was higher and the resolution increased to 0.2° (0.003 rad).

Torque and displacement using the tape recorder and X-Y plotter

The X-Y plotter had a considerably longer writing length than the chart recorder and this should have given an improved resolution. However, it was essentially a slow device and would not operate directly at the speed required. Signals were therefore transcribed to the X-Y plotter at reduced speed using the f.m. tape recorder. The tape recorder was tested in order to determine the errors that it introduced and, perhaps more important, to investigate the reproducibility of signals stored on tape.

To evaluate the error produced by the tape recorder, square wave signals corresponding in size to the torque and position signals were recorded on the X-Y plotter both directly and via the tape recorder. Use of the tape recorder lowered the resolution of the

X-Y plotter to 0.2^{o} (0.003 rad) (position) and 0.005 N m (torque).

To investigate reproducibility, a prerecorded signal was transcribed six times onto the X-Y plotter. The time interval between the first and last transcription was nine days. On each occasion the tape recorder was permitted to warm up for thirty minutes before starting transcription. It was found that the reproducibility of all points was better than 1%. There were however, shifts in the baselines of up to 3%, but as the baseline values were also obtainable from the multi-channel record this was of no importance.

Velocity

Velocity signals were obtained from two sources, differentiation of the position signal and from a tachometer. However, only the signal obtained from the differentiator circuit was routinely recorded. This was in some respects a pity, as differentiator circuits are inherently noisy, and if the amount of noise is to be kept acceptably low the band-width must be restricted.

To calibrate the differentiator, a voltage corresponding to 1 rad of potentiometer deflection was generated by a ramp generator and applied to its input. The slope of the ramp could be varied - if the ramp lasted one second the resultant differentiator output voltage represented 1 rad s^{-1}. Inspection of the differentiator output in response to different ramps showed that the response was linear from 0.1 rad s^{-1} to 10 rad s^{-1}. Empirical evaluation of error with a f.s.d. of 5 rad s^{-1} on the chart recorder was 3%. The resolution obtained in practice was less than this because the position signal is noisier than the signal that was used to calibrate the differentiator. The effect of this noise is most marked at low velocities, and in practice measurements of much less than 0.25 rad s^{-1} are not possible.

E M G

EMG records were calibrated using a commercial EMG/EEG calibrator. This produced a calibrated square wave voltage that was applied to the EMG preamplifier input.

Frequency Calibration

Many of the results called for the calculation of frequencies. To check the accuracy with which these calculations could be performed, sine wave signals at frequencies between 1 and 20 Hz were recorded on the chart recorder. The signals were supplied by a laboratory signal generator with an accuracy of 0.01% and their amplitude was similar to the signals encountered in practice. It was possible to resolve the waveform to an accuracy of 0.3 Hz between 1 and 6 Hz and 0.8 Hz between 6 Hz and 20 Hz.

In a few experiments the chart speed was doubled or increased by a factor of four; this gave a corresponding increase in accuracy. In some experiments a digital frequency meter was employed, or the waveforms were generated by the laboratory signal generator which was of known accuracy.

2.4)4 Routine calibration

An integral calibrator was used to apply calibration bars to the record. This unit supplied square wave signals to the inputs of the chart recorder. Two levels of calibration were provided (Table 2.2).

Table 2.2 Calibration pips

motor	G6M4	G9M4	G12M4
Torque (high)	0.14 N m	0.5 Nm	0.5 Nm
" (low)	0.04 N m	0.05 Nm	0.05 Nm

All motors

Displacement	(high)	1.0 rad
"	(low)	0.1 rad
Velocity	(high)	5 rad s^{-1}
"	(low)	0.05 rad s^{-1}
EMG	(high)	1 mV
"	(low)	100 μV

3) RESULTS

3.1) Sinusoidal Analysis

3.2) Detailed Study of Wrist Resonance

3.3) Compliance Measurements

3.4) Cooling of the Muscles

3.1 SINUSOIDAL ANALYSIS

3.1)1 Resonance of the limbs.

A sinusoidally varying force was applied to the limbs using an appropriate printed motor and linkage. The frequency of the applied force was automatically logarithmically increased (swept) from a low to a high value. The duration of the sweep could be varied; in the majority of experiments it occupied approximately 20 seconds, and the size of the force was sufficient to generate a large deflection of the limb.

Fig (3.1) shows the result of applying such a torque waveform to the wrist, elbow, ankle and knee respectively. The torque has a constant peak level throughout; inspection of the records show that this is not the case in the displacement and velocity traces, which show clear maxima at a certain frequency. These maxima coincide with a phase angle of 0° between the torque and velocity signal; the frequency at which they occur is therefore the resonant frequency of the system. In the examples shown, the resonant frequency of the wrist is 2.1 Hz, the elbow 0.8 Hz, the ankle 5.2 Hz, and the knee 0.9 Hz.

The limb and motor assembly comprise a torsional pendulum; any such system will resonate with a characteristic natural frequency which is controlled by the inertia of the system (J) and the restoring(spring) force (K) that it is subject to. In a linear system the equation linking these parameters is:

$$rf = \frac{1}{2\pi}\sqrt{\frac{K}{J}} \qquad (1)$$

where rf = resonant frequency (Hz)

K = spring constant (N m rad^{-1})

J = inertia (Kg m^2)

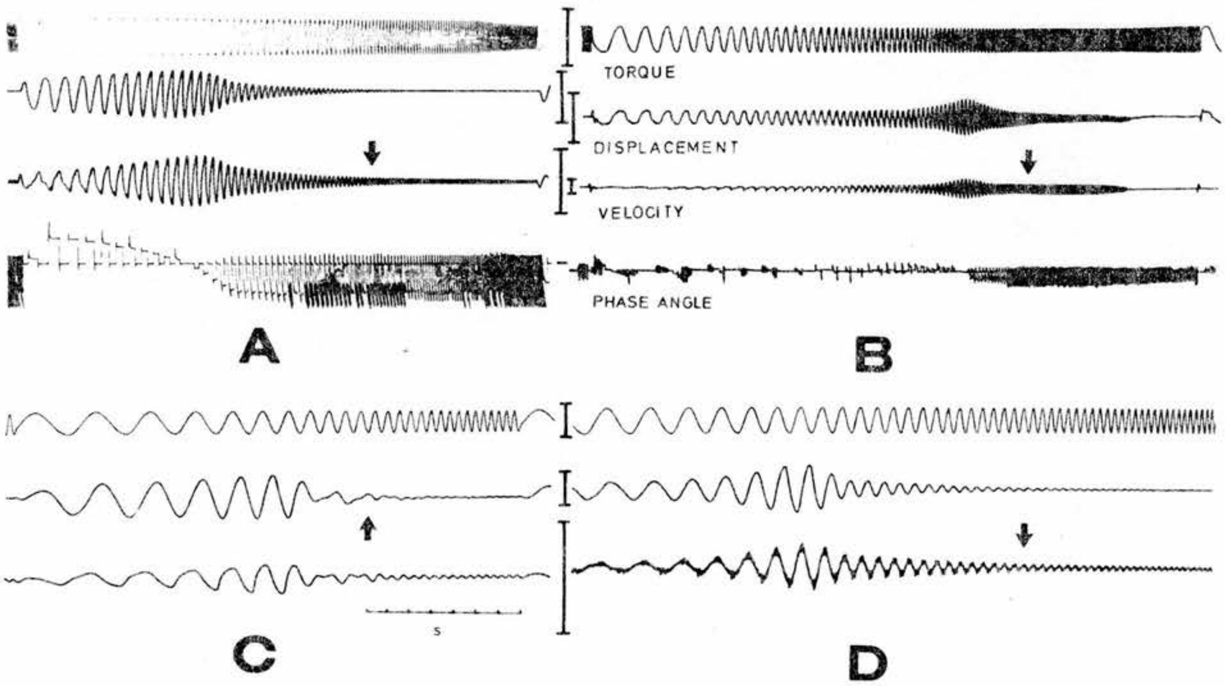


Fig. 3.1 Resonance of the limbs. The limbs are driven by a sinusoidal torque which has a constant peak value and is swept from a low to a high frequency. At a certain characteristic frequency the displacement and velocity are maximal; the phase angle between torque and velocity (shown in A and B only) is 0°. The resonant frequencies are: A (wrist) 2.1 Hz, B (ankle) 5.2 Hz, C (elbow) 0.8 Hz and D (knee) 0.9 Hz. The calibration bars represent: Torque 1.0 N m Displacement 1.0 rad, Velocity 5.0 rads^{-1}. The arrows indicate flexion direction.

The inertia of the system is due to the mass of the limb, and associated structures, which may not be contained within the limb, but move with it (some muscles, for example). The motor assembly also has some inertia, but this is small compared to the inertia of the limb.

The stiffness of the system is the viscous and elastic resistance of the structures acting at the joint; the muscles, tendons, ligaments, cutaneous tissues and the joint itself may be involved. It is very difficult to determine the relative contribution to stiffness of these different structures.

Thompson (1978) carried out an experiment in which the cadaveric human knee was progressively dissected while measurements were made of its resistance to extension and flexion and concluded that muscle was responsible for over 70% of the stiffness. However, the accuracy of this measurement is open to question, as post-mortem changes including rigor mortis had almost certainly occurred, and because the limb in question had been amputated above the knee, thus removing the large muscles of the thigh. However, in other experiments at the knee, in normal human volunteers he was able to show a correlation between muscle bulk and joint stiffness, and this has also been demonstrated by other workers at different joints. Accordingly, we feel that it is justified to refer to this stiffness as muscle tone in the same way that a clinician would refer to the resistance he experiences on passively moving a joint as muscle tone. However, the possible contribution of other non-muscular structures must be borne in mind.

The presence of the square root term in equation (1) shows that the resonant frequency is not unduly sensitive to variation of K or J. Thus to double the resonant frequency it is necessary to increase stiffness or reduce inertia by a factor of four. Conversely, as the inertia of a limb is constant, a small change in resonant frequency is indicative of a considerable change in stiffness, and this will reflect the activity of the muscles.

In principle, if the inertia of the limb was known, measurement of the resonant frequency would permit calculation of its stiffness using equation (1); (but, in a non-linear system the calculated value of stiffness may only be correct at that particular value of torque).

The moment of inertia of a body segment is dictated by its mass and radius of gyration. As the body is not of uniform density and the limbs are complicated shapes the calculation of moments of inertia presents great difficulty. In an attempt to overcome these difficulties, investigators have employed various experimental techniques but with limited success. These have been reviewed by Drillis and Contini (1966). The variability of the results of calculation of inertia by different authors, and the difficulty of applying them to the general population, were such that no attempt was made to calculate stiffness by this method; instead an alternative technique was employed and this is described in the section on stiffness and inertia measurement (3.2)8). However, if the inertia of the body segments is ranked in increasing order (data from Miller and Morrison, 1975) they can be compared with the resonant frequencies recorded. This data is set out in table (3.1).

Table 3.1 Inertia of body segment and resonant frequency

	Inertia of body segment about appropriate axis ($g.m^2$)	resonant frequency (Hz)
wrist	5.00	2.1
ankle	7.50	5.2
elbow	10.30	0.8
knee	75.90	0.9

The wrist, which has less inertia than the ankle, has a lower resonant frequency; this implies that the stiffness of the ankle must be greater. It is likely that the stiffness of the ankle is greater than that of the wrist as it is associated with considerably larger and more powerful muscles which are known to have steep tension-length curves. The resonant frequencies of the knee and elbow are almost identical; this suggests that the knee, which has greater inertia, is associated with stiffer muscles. Again, in view of the role of the knee in postural mechanisms, and the large size of the muscles attached to it this seems likely. Both the knee and elbow have a lower resonant frequency than the other joints studied, and this is certainly in accordance with their considerably greater inertia.

Berthoz and Metral (1970) applied a sinusoidally varying force to the forearm and detected a resonance at the elbow of 3-4.5 Hz. Their subjects were not relaxed as they were required to flex voluntarily with forces of up to 6 Kg. Using sinuscidal displacement inputs, Joyce, Rack and Ross (1974) found that the elbow resonated at 4 Hz, again the subject was not relaxed, and extra inertia was added by the heavy mould that transmitted force to the forearm.

Duggan and McLellan (1973) found that the relaxed elbow resonated at a frequency of 0.7 Hz, and the elbow of a subject suffering from Parkinsonian rigidity resonated at 1.2 Hz. These results were obtained by the converse method to the one employed here, the amplitude was held constant at 13.7^{o} and resonance corresponded to a minimum resisting torque. Despite this, the similarity is striking.

Using the G6M4 motor and linkage, a resonance of 17 Hz has been found for the index finger oscillating about the metacarpal phalangeal joint. Lippold (1970) found that this joint had a mechanical die away resonance of 27 Hz. Similarly, Halliday and Redfearn (1956), Randall and Stiles (1964), and Stiles and Randall (1967) detected a resonance at 25-30 Hz. The reason for the disparity is that the inertia of our apparatus loaded the finger and lowered its resonant frequency. Also, in these other experiments the finger was held voluntarily extended, rather than permitted to relax, thus raising resonant frequency. The true value therefore probably lies somewhere between 17-27 Hz. For the other, larger, joints investigated the inertia of the apparatus is negligible compared to the inertia of the limb.

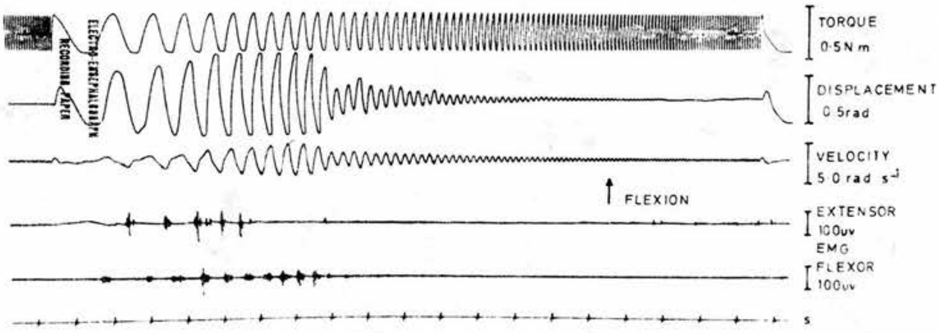
The size of the response at resonance is determined both by the size of the applied force and the amount of damping present. Thus, a large response can be indicative of a large applied force, or light damping. It is therefore impossible to determine the relative damping of the different joints investigated, as the height of the peaks cannot be directly compared. Similarly, it is not possible to calculate the magnification factor as to do this requires information about the deflection of the limb resulting from the static application of a force, and as will be shown in section 3.3)2 this cannot be determined with certainty.

In fig (3.1) the displacement generated by the sinusoidal torque waveform at the low frequency end of the sweep gives some indication of the "static response" of the limb, and permits an estimation of magnification factor. This value is approximately 2, and indicates that all the limbs are under-damped. For an under-damped system it is an acceptable assumption that the frequency at which resonance occurs when it is driven and its natural frequency of oscillation are the same (Burton, 1968).

Another "traditional" way of assessing the damping is to examine the "sharpness of tuning" or "Q" factor. A system that is lightly damped will have a "Q" that is sharper than one that is heavily damped. However, this method cannot be used to compare the results in fig (3.1) as the range of frequencies swept, and the rate of sweeping, was not the same for all the limbs investigated.

3.1)2 EMG, voluntary stiffening, and anaesthesia.

The stiffness of the musculature in normal subjects is under the control of the nervous system. This control can be reflex, voluntary or a combination of the two. Records of resonance at the wrist generally show little or no continuous EMG activity from the flexor or extensor muscles. Usually some firing of motor units is observed when the amplitude and velocity of movement is large, i.e. in the region around resonance. Fig (3.2) shows a



<u>Fig. 3.2</u> "Shortening reactions". A swept sinusoidal waveform is applied to the wrist. The chart speed has been increased to reveal the temporal relationship between EMG activity and the movement of the limb. EMG activity in the form of phasic bursts is observed; these bursts occur as the velocity of the limb is maximal, and in the shortening phase of movement. They are more prominent in the flexor muscles. The resonant frequency of this subject is 2.1 Hz. The apparent distortion of the driving waveform is due to "clipping" in the pen recorder; this is also seen in the displacement trace around resonance.
(Subject G.W.W. 45 m left wrist).

pattern of discharge of this type recorded from the wrist musculature. Inspection of the record shows that the firing of the motor units occurs during the shortening phase of movement, thus the extensors are briefly active during extension.

These "shortening reactions" are usually seen in well-relaxed subjects; they generally appear spontaneously as the subject relaxes. They are a "perverse" phenomenon - they generally disappear if the subject attempts to produce them. The classical shortening reaction ("paradoxer Muskel reaction") of Westphal (1877) has been shown by Rondot and Scherrer (1966) to be autogenic and occur when the muscle receptors in the antagonistic muscles are blocked by infusion of anaesthetic. This classical shortening reaction is thought to be present only in pathological states (Rondot and Metral, 1973).

"Shortening reactions" were observed in a large number of normal subjects tested, none of whom exhibited pathological signs. This raises two possibilities: either shortening reactions are far commoner in healthy subjects than had been supposed, or the activity may correspond to the "inverse stretch reflex" of Laporte and Lloyd (1952), as has been suggested by Denny-Brown (1962).

Stretch reflexes are not generally seen. There is sometimes evidence of phasic stretch reflexes, particularly in the flexor muscles; these invariably become less prominent as the subject becomes more relaxed. With very large torques, electrical activity may appear simultaneously in the flexor and extensor muscles; this "co-contraction" stiffens the joint and resonant frequency is consequently elevated. This may serve to protect the joint from excessive displacement.

Tonic activity in the extensor or flexor muscles is never normally seen, although there may be some background activity in the early stages before the subject relaxes. The same pattern of EMG activity has been noted at the other joints investigated. Voluntary stiffening of a limb by co-contraction of flexor and extensor muscles might be expected to raise its resonant frequency; this is shown in fig (3.3). With moderate stiffening there is a sustained tonic discharge from the flexor and extensor muscles. The amplitude and velocity of movement are much reduced and the resonant frequency is approximately trebled.

With greater degrees of voluntary stiffening several problems are encountered. It is difficult for the subject to maintain a consistent stiffness during the duration of a sweep, consequently the resonant frequency may be continuously varying. Secondly, the increased stiffness of the contracted muscles results in a very small amplitude at resonance, and this problem is compounded by the increased damping of the contracted muscles which greatly reduces the sharpness of tuning ('Q'). Detection of resonance is therefore difficult. Thirdly, the stand that supports the limb may itself resonate, interfering with the results.

Despite these difficulties, using a modified limb support system, resonances as high as 25 Hz have been seen at the wrist. This twelve fold increase in resonant frequency implies that the stiffness of the muscles has increased by a factor of 144, and illustrates the very large dynamic range of muscle. An elevation of resonant frequency has been obtained with voluntary stiffening in all the other limbs investigated.

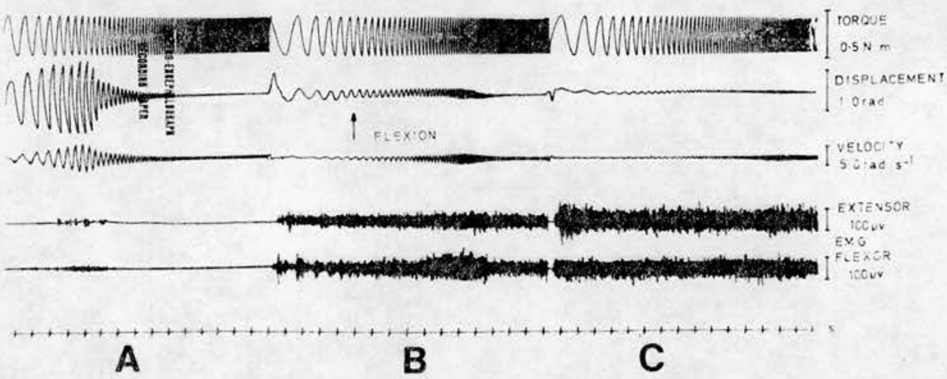


Fig. 3.3 Effect of voluntary co-contraction on resonant frequency. At 'A' the subject is relaxed with a resonant frequency of 2.2 Hz. With moderate voluntary stiffening at 'B' continuous discharge is recorded from flexor and extensor muscles and the resonant frequency becomes raised to 7.5 Hz. At 'C' the subject is very stiff; the EMG shows a further increase in amplitude and frequency, and the resonant frequency becomes 13.0 Hz. (Subject S.H. 17 f left wrist).

Comparison of the spastic and normal wrists in hemiplegic stroke patients has revealed a higher resonant frequency in the spastic limb; this is associated with a greatly increased phasic stretch reflex, particularly in the flexors. Additionally, there is generally a persistent tonic discharge in the flexor muscles at rest. This type of response is illustrated in fig (3.4).

The effects of anaesthesia and neuromuscular blocking drugs were studied in order to obtain further information about neural contribution to muscle tone. Three patients, who were candidates for elective surgery for various complaints not directly involving the neuromuscular control system of the wrist, were studied. All patients had been pre-operatively treated with diazepam (valium).

Fig (3.5) shows the resonance of the wrist of one such patient before and after anaesthesia and neuromuscular blockade. During induction of anaesthesia there was a transient period of increased EMG activity, and some involuntary movement, but there was no significant difference between the resonant frequency of the wrist before and after anaesthesia. Intravenous administration of a neuromuscular blocking drug caused no further changes, although when a depolarising drug was employed there was a substantial asynchronous burst of firing from the muscles which was sustained for about 20 seconds. On no occasion did anaesthesia or neuromuscular blockade cause a decrease in resonant frequency.

The results of the three experiments are summarised in table (3.2). From this it appears that the muscle tone in a relaxed subject is at a basal level and cannot be further reduced by procedures involving the nervous system.

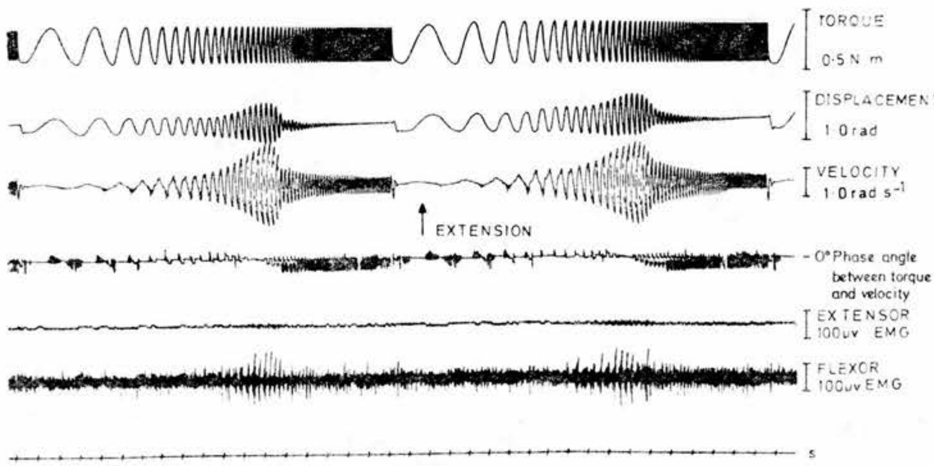


Fig. 3.4 Resonance of a spastic wrist. This subject suffered from hemiplegic spasticity following a stroke two years previously. Continuous involuntary tonic EMG is recorded from the flexor muscles. When the amplitude of movement is large, phasic stretch reflexes are superimposed on this background activity. Phasic stretch reflexes are also seen in the extensor record around resonance. The resonant frequency is elevated to 4.2 Hz. (The resonant frequency of this subject's other wrist was 2.0 Hz). (Subject W.S. 67 m right wrist).

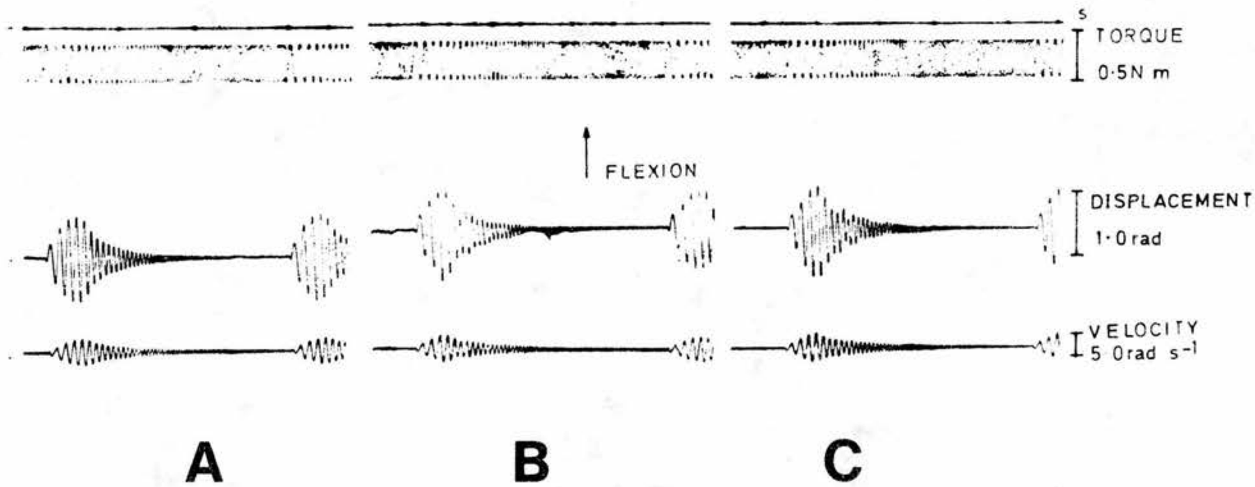


Fig. 3.5 Resonance of the wrist in an anaesthetised patient. At 'A' resonant frequency before anaesthesia is 2.4 Hz. 'B' was obtained following induction of anaesthesia with i.v. thiopentone and the resonant frequency remains 2.4 Hz. 'C' was obtained 2 minutes after the i.v. administration of 50 mg suxamethonium. Again the resonant frequency is unchanged at 2.4 Hz. The torque employed was 0.3 N m.
(Subject S.C. 41 f left wrist cholecystectomy).

Table 3.2 The effect of anaesthesia and neuromuscular-blocking drugs on wrist resonance.

Patient	Age	Sex	Pre-med	R.F. (Hz)	Anaesthetic	R.F. (Hz)	N.M. Blocking drug	R.F. (Hz)
H.R.	51	M	Diazepam	2.2	Thiopentone 300 mg Halothane	2.2	Pancuronium bromide 70 mg	2.2
A.H.	41	M	Diazepam	2.4	Thiopentone 300 mg Halothane/ N_2O/O_2	2.4	Alcuronium chloride 30 mg	2.5
S.C.	42	F	Diazepam	2.4	Thiopentone 300 mg Halothane/ N_2O/O_2	2.4	Pancuronium bromide 15 mg/ Suxamethonium 50 mg	2.4

All measurements were made with a torque of 0.3 N m

It is debatable whether these neuromuscular blocking drugs should be called muscle relaxants; their value to the surgeon lies in their ability to block troublesome cutaneous and other, deep, reflexes, but they do not decrease tone in the wrist muscles. It is, however, possible that they may have a genuinely relaxing effect on muscles elsewhere.

One criticism of these results is that the pre-operatively administered valium is known to reduce hypertonia, and it is possible that muscle tone is already sub-normal in the patients before anaesthesia. This question is taken up in section 3.2)3.

3.1)3 Ramp length, direction, and type.

In most experiments at the wrist the lower frequency of the sweep was 0.5 Hz and the upper limit 16 Hz. The frequency was automatically repetitively swept from the low value to the high value by means of a logarithmic ramp generator which drove the voltage controlled oscillator. The effects of different ramp lengths, and of reversing the direction of sweeping so that the frequency was swept from high to low, were investigated. Rate of sweeping was measured in octaves per second ($8^{ve}\ s^{-1}$), thus with a rate of 1/6 $8^{ve}\ s^{-1}$ the frequency doubled every six seconds and a scan of this range took about thirty seconds.

Fig (3.6) shows the effect of applying a torque at 0.5-16 Hz at different rates of sweeping. The torque employed was 0.5 N m. With sweeps that are longer than three seconds a clear resonance can be observed and this occurs at the same frequency in each record. With faster sweeping rates the system does not have time to "catch up" with the applied torque and the pattern of resonance is replaced by a series of irregular oscillations with "bumps"

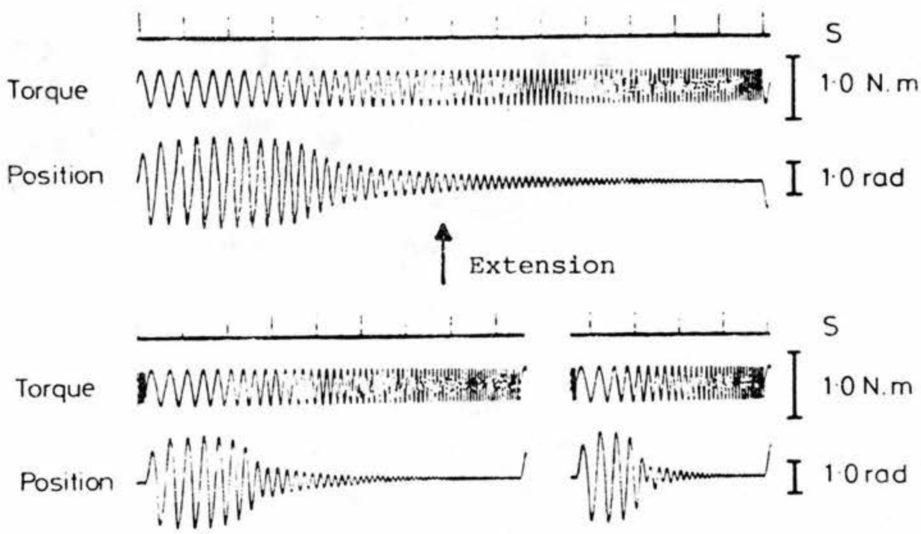


Fig. 3.6 Effect of sweep rate on resonance. The frequency was logarithmically swept from 0.5 Hz to 16 Hz at a rate of $\frac{1}{3}\,8^{ve}s^{-1}$, $\frac{2}{3}\,8^{ve}s^{-1}$, and $\frac{4}{3}\,8^{ve}\,s^{-1}$, thus taking approximately 15, 7.5, and 3.75s respectively. The resonant frequency is the same in each case (2.5 Hz). The longest sweep produces a smooth envelope; by reducing the sweep length an abrupt reduction in amplitude following resonance ("jump effect") is produced.
(Subject I.S. 45 f right wrist).

where the torque and displacement become 180° out of phase.

The system takes time to react and settle into an oscillation at the frequency of the applied force, since all the transients from the previous motion must die away before the final motion may be regarded as the response to that particular frequency. An excessively fast logarithmic frequency sweep does not allow time for this to happen, and the response of the system is complicated by the presence of these transient responses.

Accurate measurement at very short sweep lengths is therefore impossible. There is a considerable difference in the "envelope" of the displacement and velocity signals produced by sweeping at fast and slow rates. With slow sweeps a smooth envelope is produced which starts at a low amplitude and smoothly reaches a peak at resonance before declining smoothly to a minimum. With fast sweeps resonance is reached almost immediately and the amplitude and velocity of oscillation then abruptly decline by 30-50%. This sudden discontinuity in the record was named the "jump effect" (Walsh, 1975a). The jump effect, which was not observed in all subjects, always appeared at a frequency of about 2.5 Hz to 3.5 Hz i.e. just above resonance. It was not seen when the subject raised the resonant frequency of the wrist by voluntary contraction of extensor and flexor muscles. A similar jump effect has also been observed at the elbow, knee, and ankle. A jump of this type is often characteristic of an under-damped system; it has been demonstrated using a lightly damped spring/mass model (Walsh, 1975b).

Reversal of the ramp had no effect on the resonant frequency, but even at high rates of sweeping a jump was not observed.

Linearly swept frequency ramps also produced a resonance as did manually controlled sweeps employing a laboratory waveform generator. The resonant frequency determined by these different methods was the same (fig 3.7).

3.1)4 Reproducibility.

An investigation was made into the variability of resonant frequency from day to day in six subjects. This study was primarily undertaken to act as a control in an unrelated investigation into spastic hypertonia; the subjects were elderly patients who were hemiplegic following stroke. The results from the unaffected side only are reported here. The resonant frequency of the wrist was determined on a number of different occasions at an approximate average of two day intervals. The experimental conditions were similar on each occasion, the same room was employed, and testing took place at approximately the same time of day. In every case, time was allowed for the subject to settle down; tonic EMG was absent. The results of these experiments are summarised in table (3.3).

The results are consistent from day to day; the worst case (subject N.G.) has a variability of only approximately 15%. There are three possible causes for the slight day to day variation.

1) Muscle stiffness may vary slightly from day to day.
2) The variability may be a reflection of inaccuracies in measurement.
3) The positioning of the limb in the support may differ slightly on each occasion and this will affect the resonant frequency.

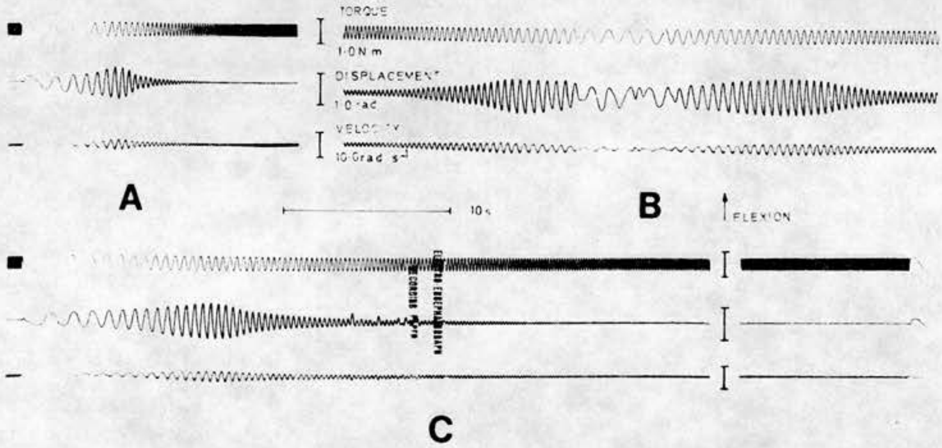


Fig. 3.7 Resonance produced by different types of sweep. At "A" resonance is produced by a "conventional" logarithmic sweep. At "B" a manually controlled decreasing and increasing frequency was employed. At "C" the range of frequencies swept is the same as at "A", but the sweep is linear rather than logarithmic. The resonant frequency is the same in each case (2.1 Hz).
(Subject G.W.W. 45 m left wrist).

Table 3.3 Analysis of resonant frequency in 6 subjects to determine day to day variability

Subject	Age (Yrs)	Sex	Wrist	Torque (N m)	Date of testing (Dec. 1980) 10	11	12	15	16	17	18	19	22	25	n	m	σ
W.S.	67	M	L	0.4	2.6	-	2.6	2.8	2.6	-	-	2.6	-	2.7	6	2.65	0.08
E.H.	72	F	R	0.3	-	2.2	2.2	-	2.1	2.1	2.0	-	-	2.2	6	2.13	0.08
F.L.	59	F	R	0.3	-	2.4	2.4	-	2.3	2.3	-	2.3	2.3	-	6	2.28	0.07
N.G.	82	F	R	0.4	2.7	2.5	-	2.5	-	-	2.5	-	2.8	2.6	6	2.60	0.10
O.C.	60	F	L	0.4	2.0	1.9	-	2.0	-	1.9	1.9	-	2.0	-	6	1.95	0.05
H.McA.	63	F	L	0.3	-	-	-	2.1	2.1	2.0	-	2.0	2.1	-	5	2.06	0.05

To obtain further information an investigation into short term variability was carried out. A very large number of normal subjects had been routinely tested for periods of up to 30 minutes; the same waveform was usually employed on a number of occasions during this period. The results of 20 of these subjects were selected and analysed for short term variability within the testing period. The results are summarised in table (3.4). This reveals a variability that is mainly within 0.2 Hz, or about 10%. Thus it seems most likely that the apparent variability is the result of inaccuracies in measurement. In an investigation of this type a reproducibility of 10-15% is quite acceptable.

Additionally, experiments have been performed regularly on certain members of laboratory staff; analysis of their records, spanning more than three years, reveals an overall consistency of about 15%.

3.1)5 Feedback induced motion.

Walsh (1975c) described a method whereby negative damping can be applied to the musculature. Under normal circumstances frictional and viscous properties of a system provide a damping force which varies in phase with the velocity and opposes the motion. If a signal proportional to velocity is generated and suitably amplified, it may be applied to the motor driving the system in such a way that the applied force is decreased, (negative velocity feedback), which effectively increases the damping. Alternatively, it may be applied to the motor in such a way as to increase the force applied, (positive velocity feedback), which reduces damping. If the damping is so reduced as to become negative

Table 3.4 Analysis of resonant frequency in 20 normal subjects on 2 or more occasions to reveal short-term variability

Subject	Age (Yrs)	Sex	Wrist	Torque (N m)	Time elapsed (mins) 0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Maximum variability %
J.W.	22	F	R	0.35	3.1		3.2					3.1								3.2
M.C.	22	F	L	0.35	2.4			2.4								2.4				0
M.L.	23	F	R	0.35	2.3		2.3			2.3					2.4				2.4	4.3
N.M.	23	F	R	0.40	2.3			2.3												0
G.W.	45	M	L	0.40	2.2		2.1					2.4			2.2			2.3		14.3
M.L.	25	M	R	0.40	2.0			1.8			1.8				1.9			1.9		11.1
E.W.	59	M	R	0.35	2.2		2.3				2.3					2.3				4.5
I.P.	22	M	R	0.35	2.5		2.6													4.0
J.C.	22	M	R	0.35	1.8			1.8				2.0								11.1
S.I.	23	M	R	0.35	2.0	2.0								2.0						0
C.P.	16	M	R	0.35	2.1		2.0													5.0
S.T.	31	M	R	0.40	2.0		2.0			2.0						2.0		2.1		5.0
W.M.	28	M	R	0.35	2.3		2.3		2.5											8.7
G.W.	17	M	R	0.35	2.8			2.8									2.2			27.3
F.McQ.	19	M	R	0.40	2.7			2.7												0
J.T.	21	F	R	0.30	2.3		2.3													0
M.J.	35	F	L	0.35	2.2				2.2											0
J.Q.	56	F	L	0.35	2.8			2.7		2.7										3.7
A.U.	52	F	R	0.30	2.1			2.1												0
A.R.	20	F	R	0.40	2.0			2.0												0

the system becomes unstable and oscillates spontaneously at its natural frequency (fig 3.8).

Positive velocity feedback was applied to all the limbs investigated, in a number of subjects. With high torque levels the resonant frequencies determined by the positive velocity feedback and swept sine wave methods are sensibly similar. In fig (3.8) the resonant frequency of the relaxed wrist is 2.1 Hz, and this same subject also had a resonant frequency of 2.1 Hz when swept sinusoidal waves were used (fig 3.1). Voluntary stiffening of the limb by co-contraction of the muscles raises the resonant frequency; this is shown in fig (3.8).

Thus, either method can be employed to determine the resonant frequency of a limb; positive feedback induced motion has the advantage that it continuously and automatically drives the limb at its resonant frequency.

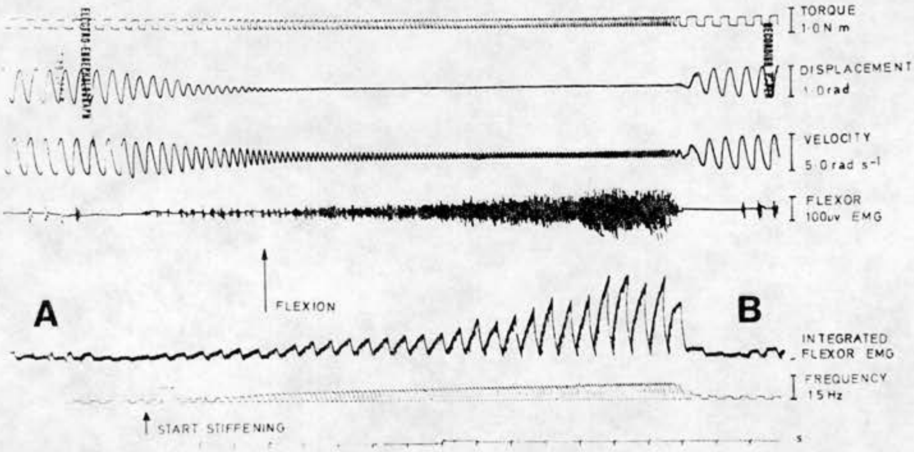


Fig. 3.8 Resonance of the wrist produced by positive velocity feedback. At "A" the subject is relaxed, the amplitude is large and the frequency low. At the point marked (arrow) the subject progressively stiffens the wrist by co-contraction. The "shortening reactions" which were seen at "A" are replaced by phasic stretch reflexes which soon become submerged in the increasing tonic activity. The amplitude is progressively reduced and the resonant frequency progressively rises. A resetting integrator is employed to indicate the amount of EMG activity in successive 0.5 s epochs, and a frequency meter gives a record of instantaneous frequency. At "B" the subject relaxes again and the shortening reactions reappear. Similar records have been produced sampling EMG activity from the extensor muscles.
(Subject M.L. 27 m left wrist).

3.2 DETAILED STUDY OF WRIST RESONANCE

3.2)1 Introduction

An investigation was carried out in 23 subjects to study in detail the biodynamics of the wrist musculature, and establish the variability of the responses between different subjects, and between left and right wrists. 12 of the subjects were male, and one male subject and one female subject were left-handed.

The age of subjects ranged from 13 to 58, the majority were aged between 20 and 25. There was a wide range of body builds and occupations, although no trained athletes were investigated. All subjects were apparently neurologically normal.

3.2)2 Swept sine waves

A logarithmically increasing sinusoidal waveform at different torque levels was applied in turn to each wrist; the sweep rate used in most of the experiments was 1/6 8^{ve} s^{-1}. The applied torque, resulting displacement and velocity, and, in the early experiments, the phase angle between torque and velocity, were recorded. In all cases 10 values of peak torque between 0.05 N m and 0.35 N m were used; frequently other values of torque were interposed at the lower end of the scale or added at the higher end. For each subject there was therefore a record of the behaviour of both wrists at at least 10 different torque levels. In fact, particularly in the earlier experiments, several sweeps were often made at each torque level.

The results were treated in the following way. Each of the 46 wrists had the following three parameters tabulated at each of the 10 (or more) values of peak torque.

1) resonant frequency (the frequency for which displacement and velocity were maximal and the phase angle between torque and velocity was zero (in Hz)).

2) peak amplitude at resonance (in rad).

3) peak velocity at resonance (in rad s^{-1}).

Where more than one sweep had been carried out at a particular value of torque the results of the sweeps were averaged, although in practice the variability was extremely small. Thus, there were three parameters tabulated for at least 10 different torque levels in 46 wrists, more than 1300 values in all: to analyse this large amount of data a computer and statistics programme were employed.

3.2)3 Resonant frequency - non-linear stiffness

Fig (3.9a) shows the resonant frequency of one male subject at 10 different torque levels. For moderate values of torque the resonant frequency is almost constant, in this case with a value of 2.5 Hz. Below a certain threshold value of torque (0.23 N m) the resonant frequency increases, becoming inversely related to the frequency. The reciprocal relationship is illustrated in fig (3.9b). This pattern of resonant frequency suggests that if the wrist is considered as a spring, its stiffness is constant for moderate to high torques, but becomes considerably greater and non-linear as the torque is reduced. A similar pattern of increasing stiffness for small torques has been reported previously for the wrist (Walsh, 1973 and Lakie and Tsementzis, 1979).

There is a sharp division between the two types of behaviour; the wrist acts as a "softening spring" up to a certain critical torque ("torque threshold") after which it behaves in a linear way. Larger (0.8 N m) torques have been employed and although the

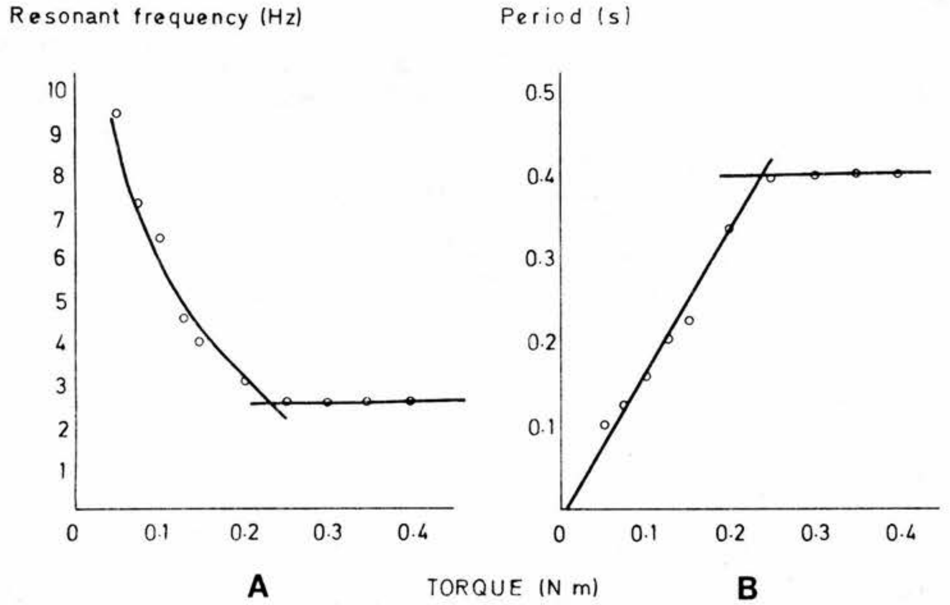


Fig. 3.9 Resonant frequency of wrist vs torque. (A) Resonant frequency at 10 different torque levels. The sharp discontinuity between the linear and non-linear regions is evident; this is emphasised by drawing two distinct curves. The intersection of the two curves is the "torque threshold" (0.23 N m). (B) the same data but with the reciprocal of frequency (Period) on the ordinate. Again, the two lines intersect at the torque threshold. The reciprocal relationship of torque and resonant frequency with torques lower than the "threshold" is illustrated. (Subject W.M. 28 m left wrist).

amplitude of movement becomes very large (sufficient to reach the anatomical limits of the joint) there is no further decrease in resonant frequency; indeed an increase has sometimes been observed due to semi-voluntary stiffening of the muscles. This is easily detected in the EMG record.

When the experiment was repeated on a female subject, the resonant frequency with moderate values of torque was similar to that observed in a male subject, and the same pattern of non-linearity was seen when the torque was reduced below a critical threshold value. The torque threshold, however, was considerably lower than that of a male subject (cf. Tsementzis et al., 1980).

To investigate the statistical significance of this sex difference and non-linearity, an analysis of variance was performed: the results of this are tabulated (table 3.5). Both sex and torque are sources of variation ($p < 0.01$) and they interact. There is no significant difference between left and right wrists. In fig (3.10), mean curves for male and female resonant frequencies have been plotted using this data. The results from left and right wrists are pooled. The two curves are similar, except that the threshold value of torque is lower for female subjects. The difference between the curves becomes statistically significant ($p < 0.05$) at torques less than 0.175 N m.

At torque levels above 0.25 N m, all the wrists investigated acted in a linear way. The scatter at these high torque levels was small; at 0.30 N m for example, the resonant frequency for males was 2.3 Hz (s.d. 0.18) and for females 2.5 Hz (s.d. 0.17). These values are not significantly different. At this torque level the highest resonant frequency encountered was 2.8 Hz and the lowest

Table 3.5

Variate: Resonant Frequency

Analyses of Variance

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F-Ratio	
Sex	29.96	1	29.96	9.7	$p < 0.01$
Error	65.12	21	3.10		
Torque	1350.42	9	150.05	202.1	$p < 0.01$
Hand	0.05	1	0.05	0.1	n.s
Interaction: Sex x Torque	58.49	9	6.50	8.8	$p < 0.01$
Interaction: Sex x Hand	0.01	1	0.01	0.0	n.s
Interaction: Torque x Hand	1.08	9	0.12	0.2	n.s
Interaction: Sex x Torque x Hand	6.40	9	0.71	0.9	n.s
Error	273.22	368	0.74		
Total	1784.76	428			

Table of Means

Torque	0.05	0.075	0.10	0.125	0.15	0.175	0.20	0.25	0.30	0.35	S.E.
Male	8.657	6.416	4.526	3.789	3.105	2.826	2.353	2.271	2.253	2.254	0.184
Female	7.160	4.647	3.510	2.921	2.623	2.481	2.481	2.478	2.487	2.552	0.176

S.E. of Differences in Mean of Male and Female = 0.292

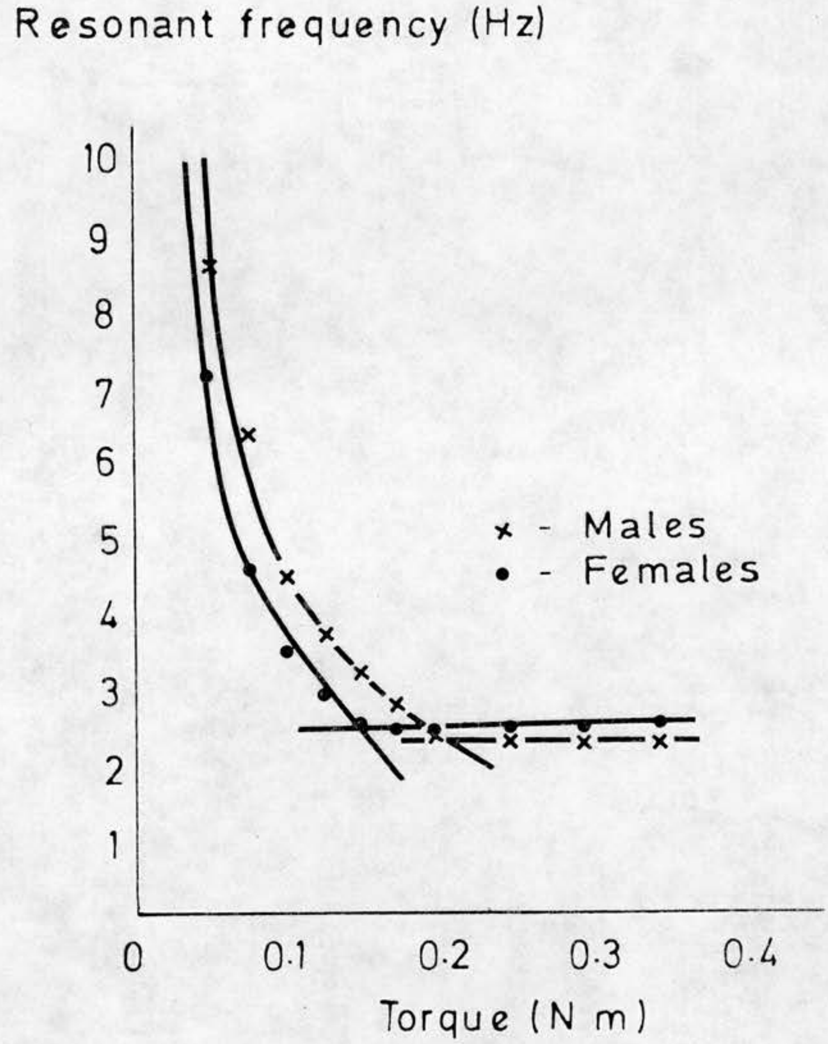


Fig. 3.10 "Mean curves" for male and female subjects. The mean values of resonant frequency of the wrist are plotted at 10 torque levels. The standard error for differences in the mean is 0.292. Thus the curves become significantly different ($p < 0.05$) at 0.15 N m and lower torques, and are not significantly different with larger torques. The mean torque thresholds for men and women are 0.22 N m and 0.14 N m respectively.

1.8 Hz, and all the wrists investigated behaved as a reasonably homogenous group. When the torque level was reduced, all the wrists resonated at a higher frequency; this change-over from a linear system to a non-linear system occurred at a higher value of torque (torque threshold) in the male subjects than in the female subjects.

To emphasise this, the torque threshold values were determined for each wrist and are shown in fig (3.11), which also shows the mean values for the male and female groups. These values are (to 2 significant figures): male torque threshold (right wrist) 0.22 N m, (left wrist) 0.22 N m, female torque threshold (right wrist) 0.14 N m, (left wrist) 0.14 N m. This fig shows the sex difference in torque thresholds - there is however some overlap; two men have anomalously low values for their left wrists, and one man has an anomalously low value for the right wrist. There is no systematic difference in the torque thresholds of left and right wrists.

At very low torque levels the system becomes very broadly tuned, the amplitude is low, and a precise resonant frequency cannot be established. However, the resonant frequency of both males and females was sometimes greater than 10 Hz at the lowest levels investigated.

Fig (3.12) illustrates the way in which resonant frequency is dependent on driving torque, and it also shows the very great reduction in amplitude at resonance, and broad tuning, with small torques. The wrist is a complex system which behaves in a linear way when the applied torque is large, and acts as a non-linear stiffening spring when the torque is reduced. Additionally there is a sex difference in the point at which transition from linear to non-linear system occurs, although with the small number of

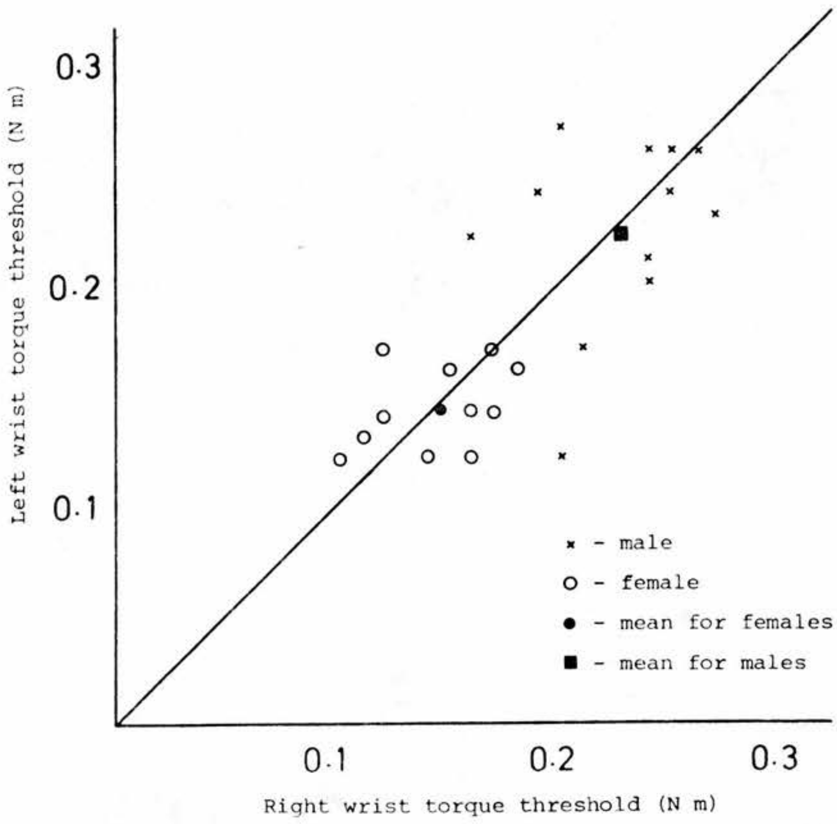


Fig. 3.11 Torque threshold for left and right wrists of male and female subjects. These values were calculated graphically as in fig. (3.9b). The mean values for male and female subjects were 0.22 N m and 0.14 N m respectively. The mean values are not significantly different for left and right wrists, and the left and right values are equally distributed. There is only a small overlap between male and female values; two male subjects have values for the left wrist that overlap female subjects, and one male has a "female" value for his right wrist.

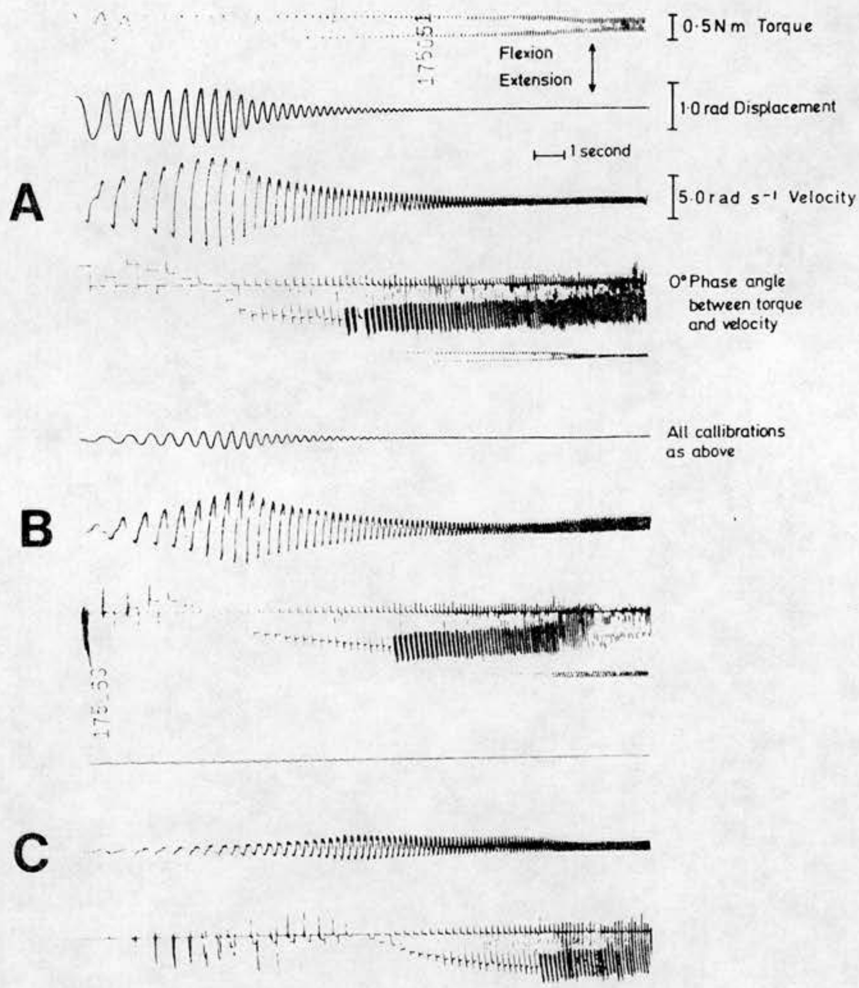


Fig. 3.12 Resonance of the wrist at 3 torque levels. In "A" the torque is 0.4 N m; this is successively halved in "B" and "C". The resonant frequency in "A", "B" and "C" is 1.9 Hz, 2.0 Hz and 5.3 Hz respectively. The amplitude and velocity at resonance are also non-linearly related to torque; the reduction in amplitude from "B" to "C" is greater than from "A" to "B". This disproportionately heavy damping at low torques is reflected in the low "Q" in "C".
(Subject M.A.L. 25 f left wrist).

subjects tested this difference is only just significant and there is some overlap.

Muscle tone has therefore been shown to be critically dependent on the size of the force employed to measure it. For small forces the muscles are very considerably stiffer than they are for large forces. Furthermore, above a threshold value of force, the behaviour of the postural system is linear; below this level it is decidedly non-linear. From a teleological viewpoint, this increased muscle stiffness for small applied forces **may be** a "useful" phenomenon: it makes the task of the controlling nervous system much easier by reducing the susceptibility of the postural system to externally applied perturbation. The elucidation of this pattern of non-linearity is fundamental to this thesis.

As male hands are generally larger, and have more inertia than female hands, the effect of increasing the inertia of a female hand was investigated. A steel bar (moment of inertia 2.5 g. m^2) was added to the system and the experiment repeated. Predictably, the resonant frequency of the system was reduced, but rather than raising the threshold value of torque to the same level as that of a male subject, the threshold value was further decreased (fig 3.13).

A small study was carried out on 11 young children, four of whom were brothers. Seven were male. Each child had a female resonance pattern except one, a boy of 13 years old, who was pubertal.

When subjects went as stiff as possible, their resonant frequency was considerably elevated, and variations in torque were without effect on the resonance of the wrist. The same elevation of resonant frequency and independence of torque and resonant frequency

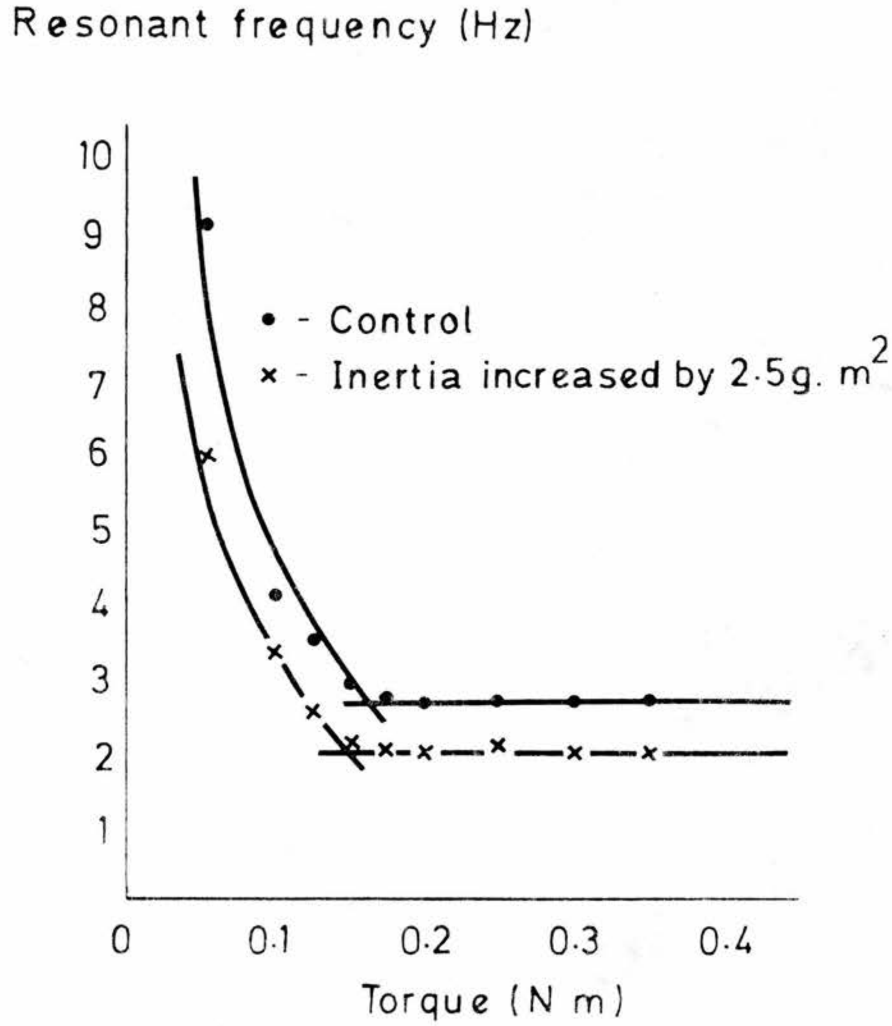


Fig. 3.13 Female wrist with and without added inertia. Additional inertia 2.5 $g.m^2$ was added in an attempt to simulate a male wrist. The resonant frequency is reduced at all levels of torque, but the torque threshold is slightly decreased and is not elevated to a male level.
(Subject S.P. 36 f left wrist).

was noted in a number of stiff spastic stroke patients.

At the rate of sweeping employed in these experiments ($1/6\ 8^{ve}\ s^{-1}$) a jump effect was observed in 14 of the 23 subjects. It was most prominent with larger values of torque (greater than 0.25 N m) and was occasionally present at only one wrist. Interestingly, it was seen in all but one of the female subjects and only four of the 11 male subjects. It always appeared at frequencies of 2.5 - 3.5 Hz, a range just above the critical resonant frequency of the wrist.

One male patient and one female patient were tested at six different levels of torque, during anaesthesia and after treatment with neuromuscular blocking drugs. Control measurements were previously obtained. There were no significant differences in the record after anaesthesia or treatment with neuromuscular blocking drugs. These patients had been treated pre-operatively with diazepam. This drug is known to be effective in reducing muscle hypertonia; it is therefore possible that the muscle tone of the patients tested was already sub-normal before anaesthesia. Comparison of the record obtained from these patients before anaesthesia with those obtained from the normal volunteer subjects revealed no significant differences. In fig (3.14) the curves obtained from the female subject before and after anaesthesia and neuromuscular blockade are superimposed on the mean curve for female subjects taken from fig (3.10).

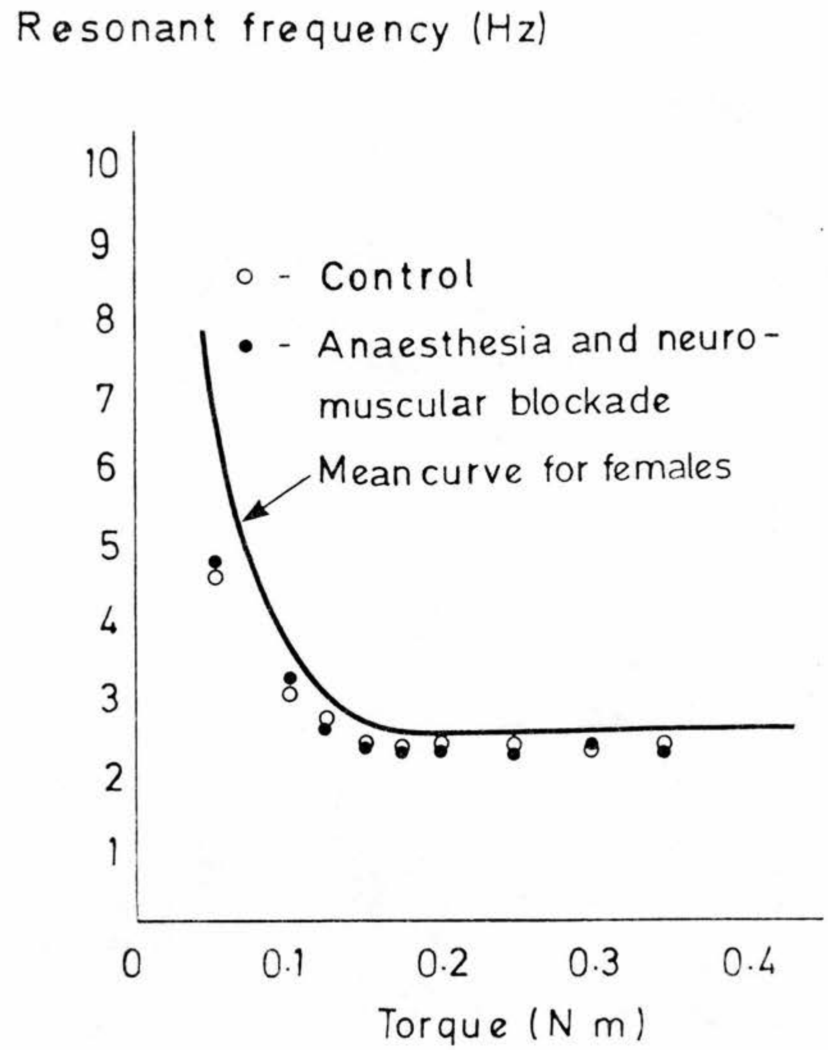


Fig. 3.14 Torque vs resonant frequency of an anaesthetised subject. There is no significant change in resonant frequency at any torque level following anaesthesia and neuromuscular blockade. The pattern obtained is very similar to the "mean curve" for female subjects taken from fig. (3.10).
(Subject R.G. 22 f left wrist laminectomy).

3.2)4 Amplitude and velocity at resonance - damping.

The amplitude at resonance is controlled by the size of the applied force and by the damping in the system; at resonance with zero damping the magnification factor will be infinite. Therefore, with linear damping, a plot of amplitude at resonance versus driving torque should be a straight line.

An analysis of variance was carried out on the peak amplitude at 10 different torque levels (table 3.6). The peak amplitude varied significantly ($p < 0.01$) with torque and sex and the two interacted. There were no significant differences between left and right wrists. In fig (3.15) mean curves have been plotted for male and female subjects, using this data. The damping is apparently non-linear, being disproportionally heavy for the smallest torques. A considerable sex-difference is apparent; the peak amplitude in females is 50 - 100% greater than in males at the same torque level, and this difference is significant ($p < 0.05$) at torques greater than 0.10 N m. The non-linear damping at low torque levels is artefactual, and due to static friction in the motor.

In fig (3.15) the torque threshold values for male and female subjects have been indicated. These values correspond to a displacement range of 0.31 rad to 0.36 rad in both men and women. It might therefore appear that as the transition to greater stiffness occurs at approximately the same amplitude in both groups it is possible to refer to a single critical amplitude rather than two threshold torques. The transition from a stiff non-linear system to a less stiff linear one would then occur at a critical displacement of between 0.31 and 0.36 rad in both men and women.

Table 3.6

Variate: Peak Amplitude

Analyses of Variance

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F-Ratio	
Sex	10.18	1	10.18	90.1	$p < 0.01$
Error	2.37	21	0.11		
Torque	28.80	9	3.19	607.1	$p < 0.01$
Hand	0.0005	1	0.0005	0.1	n.s
Interaction: Sex x Torque	3.66	9	0.41	77.1	$p < 0.01$
Interaction: Sex x Hand + Torque x Hand	0.01	10	0.001	0.3	n.s
Interaction: Sex x Torque x Hand	0.01	9	0.002	0.37	n.s
Error	1.94	368	0.0527		
Total	46.97	428			

Table of Means (x 10^4)

Torque	0.05	0.075	0.10	0.125	0.15	0.175	0.20	0.25	0.30	0.35	S.E.
Male	255	359	650	959	1491	1796	2377	3414	4332	5141	154
Female	336	752	1804	2846	4237	5439	6679	8500	9858	11,400	148

S.E. of Differences in Mean of Male and Female = 374

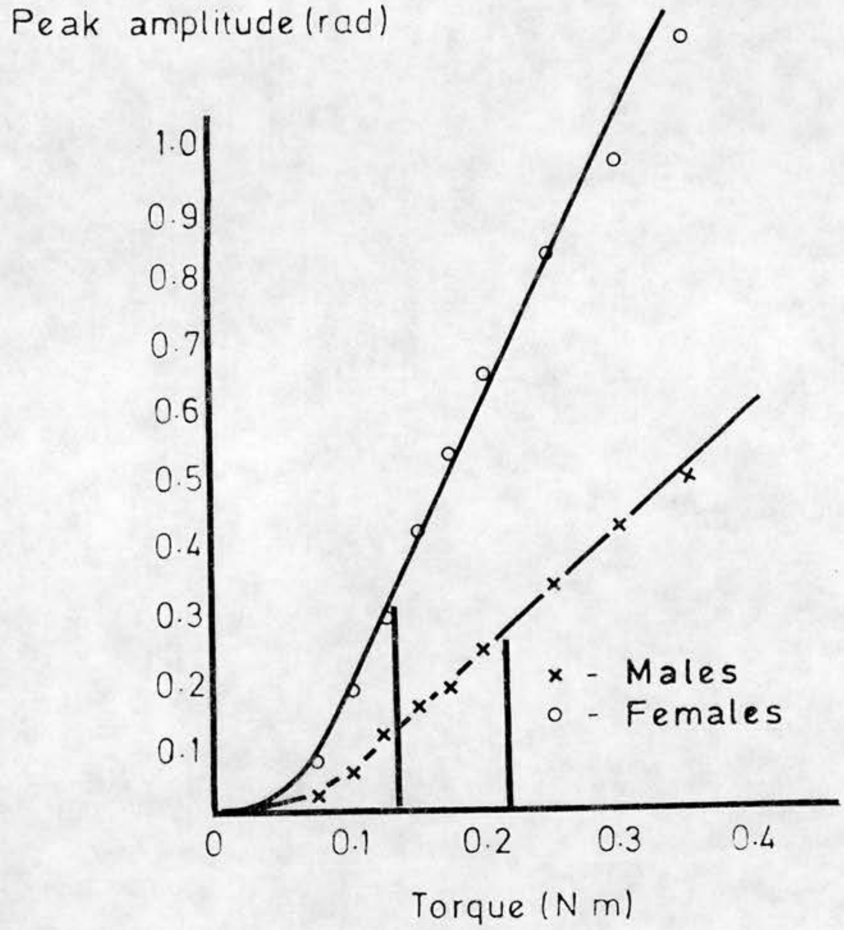


Fig. 3.15 Peak amplitude at resonance of male and female subjects. Results from both wrists are pooled. At all levels of torque the amplitude achieved by female subjects is greater than that achieved by male subjects. This difference is significant ($P < 0.05$) at torques greater than 0.10 N m. The damping is effectively linear at torques greater than 0.1 N m and 0.06 N m for male and female subjects respectively. The "torque threshold" values for male and female subjects are indicated; they both correspond to an amplitude range of 0.31 to 0.36 rad.

However, in a resonating system, the displacement and velocity are directly related, so it is also possible that the transition may be linked to a critical velocity. Accordingly, similar analysis was performed for peak velocities at resonance, and mean curves for the male and female group are shown in fig (3.16).

The velocity curves parallel the displacement curves. The damping is appreciably non-linear at the lowest torques (again this is an artefact caused by static friction). The torque threshold values have been indicated, and they correspond quite well to a single range of velocity, between 1.5 and 2.1 rad s^{-1}. To summarise these results:

1) The postural system is stiffer for small displacements than large ones. This is shown by the elevation of resonant frequency as the torque is reduced below a critical "threshold level" which is significantly lower for female subjects. The mean threshold level for male subjects is 0.22 N m and for female subjects 0.14 N m.
2) There is evidence of non-linear damping in the system. At the lowest torque levels (less than 0.1 N m) the peak velocity and displacement are disproportionately low. Similarly at the lowest torque levels the system is apparently very broadly tuned. This distortion is due to static friction in the motor.
3) At all torque levels damping is heavier in male subjects than in females; this is shown by the smaller peak displacements and velocities at resonance attained by male subjects at each torque level.

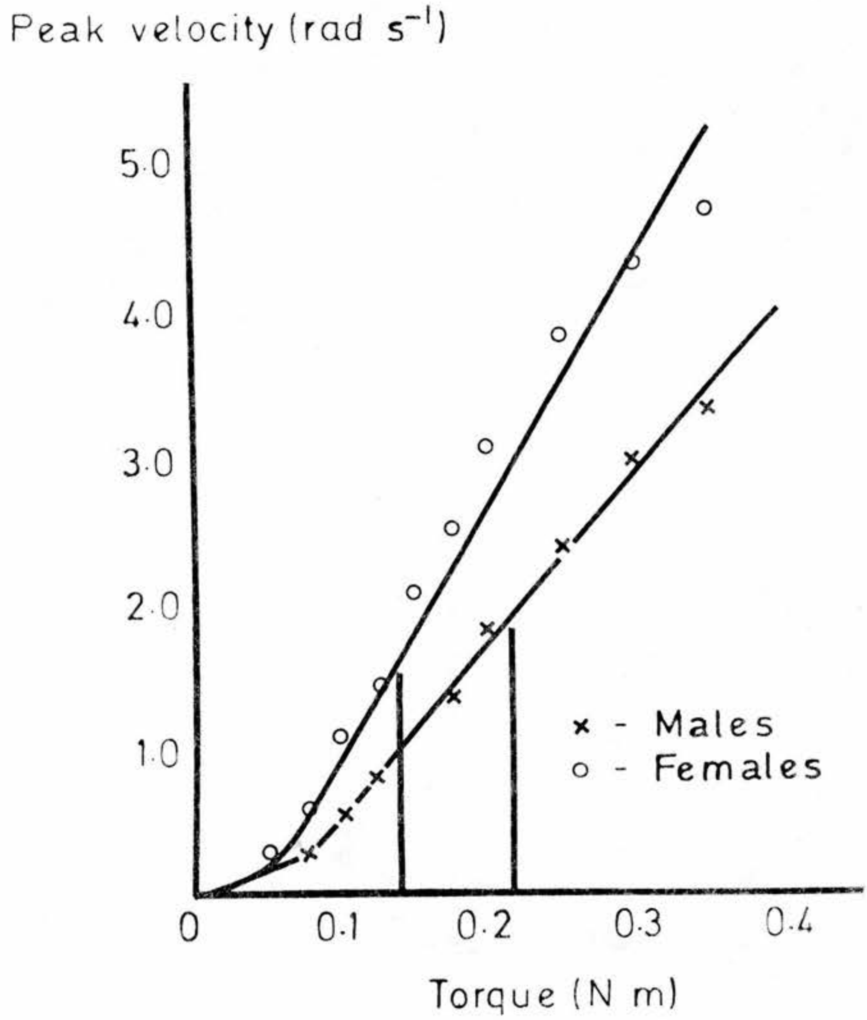


Fig. 3.16 Peak velocity at resonance of male and female subjects. Right wrists. At all torque levels the peak velocity is higher for female subjects than male subjects. This difference is significant ($P < 0.05$) at torques greater than 0.10 N m. The transition to heavy damping occurs at approximately 0.1 N m and 0.06 N m for male and female subjects respectively. The "torque threshold" values for male and female subjects are indicated; they both correspond to a velocity range of 1.5 to 2.1 rad s^{-1}.

4) When the torque threshold values of 0.23 N m and 0.14 N m for the male and female groups respectively are evaluated on the peak amplitude and peak velocity curves (figs 3.15 and 3.16) they correspond quite well to a single critical displacement and velocity. The critical amplitude range is 0.31 to 0.36 rad, and the critical velocity range is 1.5 to 2.1 rad s^{-1}. At this critical amplitude or velocity in men and women the postural system of the wrist changes its behaviour from stiff and non-linear to less stiff and linear.

5) The sex difference in torque thresholds reflects the extra torque that is required in male subjects in order to attain the critical amplitude or displacement.

6) The sex difference in the torque thresholds must reflect a qualitative or quantitative difference in the muscles, or conceivably the joint.

7) Young children have a female pattern of resonant frequency and peak amplitude and this changes at puberty to a male pattern in male subjects. Hormonal factors may be involved.

8) Anaesthesia and neuromuscular blockade do not alter any of the measured parameters in a significant way. The nervous system does not contribute to relaxed muscle tone in a relaxed subject. This is supported by observation that the EMG in normal subjects is normally silent, tonic stretch reflexes are never seen, and phasic stretch reflexes appear only transiently at high force levels. Shortening reactions are seen quite frequently, but they are a variable phenomenon, and apparently do not alter the mechanical parameters that were measured.

3.2)5 Positive velocity feedback

The use of positive velocity feedback at different torque levels was investigated. Problems were sometimes encountered at low force levels with the G9M4 motor as this relied on differentiation of the displacement signal to provide a velocity input. With small torques the velocity signal fell below the signal to noise ratio of the potentiometer/differentiator combination, and reliable self sustaining oscillation did not occur. This difficulty was overcome by employing a G6M4 motor which was coupled to a tachogenerator capable of providing a low noise signal down to very low velocity levels. Oscillation was reliable and self sustaining with the lowest torque employed; as the motor was smaller the maximum torque was limited to 0.3 N m.

The resonant frequencies obtained using positive velocity feedback and swept sinusoidal analysis at different torque levels were compared in four subjects; the results of these experiments are summarised in table (3.7). With torques less than 0.20 N m the resonant frequencies given by the two methods are sensibly similar, but at higher torques the resonant frequency using swept sinusoidal wave forms is slightly higher than that given by feedback induced resonance. The difference is not however significant and is of no importance in a system where the reproducibility is of the order of 10-15%.

A likely explanation for this difference is that, when positive velocity feedback is employed, saturation in the output stages of the power amplifier causes the applied wave form to approximate to a square wave rather than a sinusoid. The application of a square wave force to a resonating system can give different results to those

Table 3.7 Swept sinusoidal wave vs. positive velocity feedback.

	swept sine wave				+ve vel. feedback			
SUBJECT	W.M.	M.L.	R.D.	J.W.	W.M.	M.L.	R.D.	J.W.
SEX	M	M	F	F				
AGE	28	27	24	22				
TORQUE (N m)								
0.05	9.9	8.7	8.6	7.8	9.6	8.9	8.3	8.0
0.10	5.2	3.5	4.8	3.4	5.5	3.7	4.9	3.5
0.125	-	-	3.2	3.0	4.4	-	3.4	-
0.15	2.7	2.1	2.6	2.5	2.8	2.3	2.7	2.4
0.175	2.2	-	-	2.5	2.2	-	-	2.4
0.20	2.2	2.0	2.5	2.5	2.1	2.0	2.6	2.3
0.25	2.2	2.0	2.5	2.5	2.0	2.1	2.4	2.3
0.30	2.2	2.0	2.5	2.5	2.0	2.1	2.4	2.3
0.35	2.2	2.0	2.5	2.5	2.0	2.0	2.4	2.3
0.40	2.1	2.1	2.5	2.5	2.0	2.0	2.3	2.4
0.45	2.1	2.1	2.5	2.5	2.0	2.0	2.3	2.3
0.50	2.1	2.0	2.5	2.5	2.0	2.0	2.3	2.3

All frequencies in Hz.

produced by the application of sine waves. When swept square waves have been substituted for swept sine waves, a slight reduction in resonant frequency has sometimes been noted and this lends support to the above theory. For all practical purposes the difference between swept sine waves and positive velocity feedback resonance is negligible; both can be used to measure the resonant frequency of the postural system.

3.2)6 Displacement bias.

In all the experiments so far described the movement of the limb took place about its natural resting place. In some subjects this approximated to a straight ahead position; the wrist angle was 180°. The majority of subjects adopted a position in which the wrist was slightly flexed and it thus approximated better to the mid-point of the available range of movement. It was noted that female subjects almost invariably had a greater ability to extend the wrist than male subjects; some could voluntarily execute flexion/extension movements of more than 180°.

The effect on resonance of varying the resting position of the wrist was investigated by means of superimposed biasing torques. A d.c. current was passed through the motor which generated a constant force thus biasing the wrist into flexion or extension. Care had to be taken not to employ an excessive biasing torque or the output stages of the amplifier overloaded, causing distortion of the waveform.

When large biasing torques (greater than 0.4 N m, giving a displacement of more than 0.5 rad flexion or extension) were applied to the wrist in the absence of a superimposed waveform, no additional EMG activity was observed; tonic stretch reflexes were never seen.

The effect of such a bias superimposed on swept sinusoidal waves is illustrated in fig (3.17). With this large amount of bias, giving a displacement from the resting position of more than 0.5 rad, there is a very slight increase in resonant frequency in both the flexion and extension positions. The peak amplitude and velocity at resonance is decreased. No tonic stretch reflexes have been seen, even with large biasing forces. There is sometimes, however, phasic stretch reflex activity in the muscles that are subjected to the extra stretch. This is evident in the flexor record in fig (3.17), and is prominent only when the amplitude of movement is large, that is, around resonance. Similar results have been obtained using positive velocity feedback to induce resonance. With smaller amounts of bias (less than 0.25 rad) there are no changes in resonant frequency, amplitude, or EMG.

The effect of bias on the resonant frequency vs. torque curve is illustrated in fig (3.18). No significant difference is produced by biasing the wrist by 20^{o} (0.34 rad) into either flexion or extension. The total range of flexion/extension movement at the wrist in this subject was 160^{o} (2.80 rad); the amount of bias employed must therefore have changed the length of the muscles by about 25%. Despite this change in length the torque threshold remains unaltered. The torque threshold cannot therefore represent the amount of torque required to attain an absolute length at which the system changes from non-linear to linear stiffness.

An alternative method of displacing the wrist from its natural equilibrium position was investigated in two subjects. The subject observed a spot on a large screen oscilloscope; the movement of

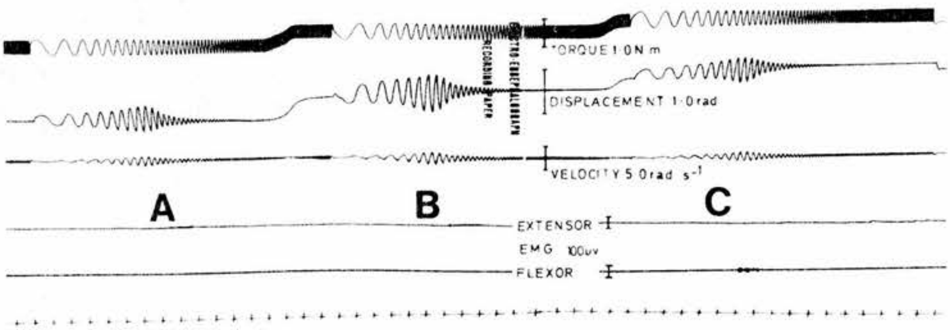


Fig. 3.17 Bias experiment. At "B" there was no bias; movement occurred about the natural resting position. At "A" the wrist was biased 0.65 rad (37°) into flexion and at "C" 0.50 rad (29°) into extension. The same biasing torque (0.40 N m) was employed in both directions; the wrist is stiffer in extension than flexion. The extra stretch applied to the flexor muscles in "C" elicits slight phasic stretch reflex activity around resonance. Flexion and extension bias of this size raises the resonant frequency from 2.1 Hz at "B" to 2.5 at "C" and 2.3 at "A". The amplitude at resonance is also reduced at "A" and "C".
(Subject B.M. 22 m right wrist).

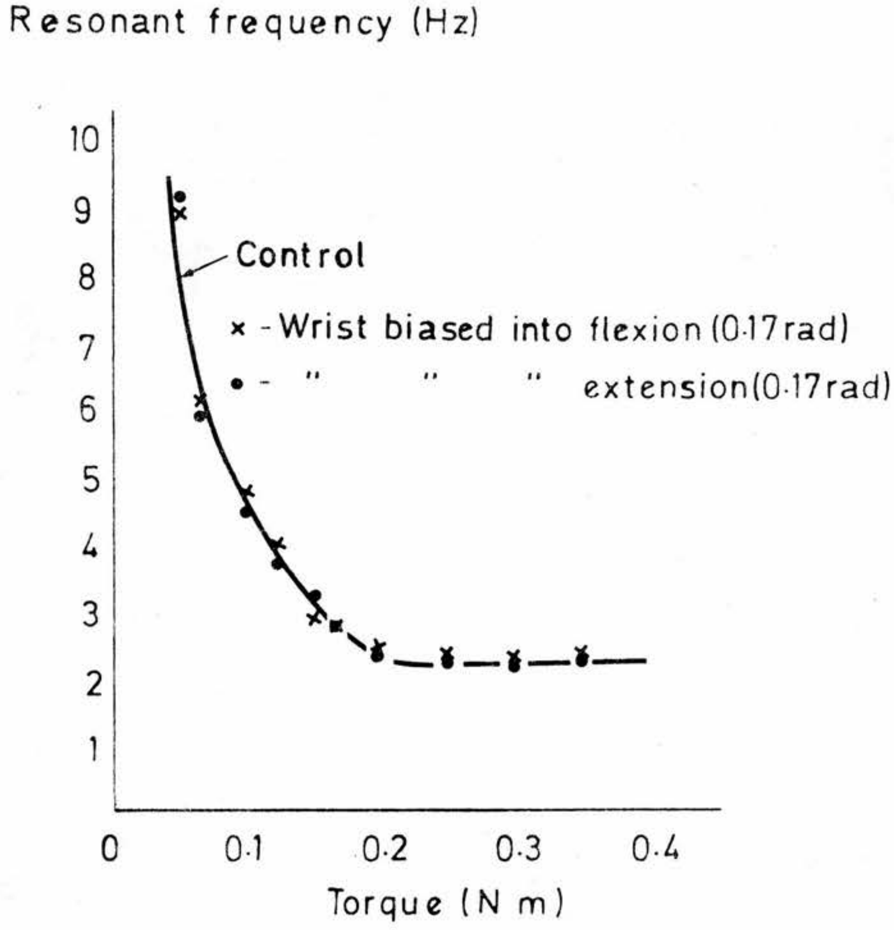


Fig. 3.18 Bias experiment; torque vs resonant frequency. The control curve was plotted from measurements of resonant frequency at 10 torque levels; movement occurred about the natural resting position of the wrist. The resonant frequency of the wrist with these same torques is shown following a bias of 20^{o} (0.34 rad) into flexion and extension. The pattern of non-linearity is not changed by this manoeuvre.
(Subject E.G.W. 57 m right wrist).

the spot was controlled by the position of the wrist measured by the potentiometer attached to the motor shaft.

Heavy electrical damping was applied to the oscilloscope deflection circuits; the spot therefore indicated the mean position of the wrist. With practice, using this method, it was found possible to maintain the mean position of the wrist to within about 5° of any desired position.

When the position of the wrist was changed in this way by even a small amount both subjects exhibited co-contraction of flexor and extensor muscles. Thus, the new resting position of the wrist could only be maintained at the expense of some stiffening of the joint, and this was reflected in an elevation of the resonant frequency. The rise in resonant frequency was roughly proportional to the degree of displacement that was made.

3.2)7 Mechanical model.

In order to check the linearity of the apparatus, a model was used. The model consisted of a flat plate torsional spring (spring constant 1.25 N m rad^{-1}) and a steel bar (inertia 5 g. m^{2}). These parameters were similar to those of the wrist joint. Damping was provided either electrically, by negative velocity feedback applied to the motor, or mechanically by an air vane, which provided a retarding force that was related to velocity. The amount of damping was sufficient to arrest the motion of the model after two or three oscillations. If the model was manually perturbed a damped oscillation of two or three cycles with a frequency of 2.6 Hz resulted.

When the system was driven by a ramped sinusoidal wave a resonance at 2.6 Hz was encountered; the resonant frequency was the same at all levels of torque. The "Q" was decreased at low torque levels; this was almost certainly a reflection of static friction in the motor. The G9M4 motor had appreciable "stiction", and it is likely that the G6M4 motor would have given a better result. However, the model could not conveniently be attached to this motor.

When biasing torques were applied to the model there was no change in resonant frequency. The amplitude of oscillation of the model at resonance could be reduced by increasing the damping, either by increasing the gain of negative velocity feedback, or by enlarging the air vane. Conversely, if the damping was decreased, the jump effect became very prominent, particularly if fast sweep speeds were employed. When positive velocity feedback was applied to the model it oscillated, and the frequency of this oscillation was also 2.6 Hz.

3.2)8 Measurement of wrist stiffness (and inertia of the hand) employing resonant frequency analysis.

It has been shown that the oscillating wrist behaves as an underdamped torsional pendulum. With moderate torque inputs between 0.25 N m and 0.5 N m its behaviour is linear. The resonant frequency is easily established, but the values of stiffness (K) and inertia (J) are unknown.

One way of establishing the size of these parameters is to alter experimentally the inertia or stiffness of the system by a known amount. The inertia of a system can be altered by the use of positive or negative acceleration feedback, but generation of a "clean" signal proportional to acceleration is difficult in practice, and a simpler approach was used. The inertia was increased by the addition to the system of steel bars of known inertia. Thus, only the effect of increased inertia was investigated. The stiffness of the system can be altered by the use of positive or negative displacement feedback; with negative position feedback the motor simulates a spring, the stiffness of which is dictated by the gain of the feedback loop, and the system becomes self-centering. Positive position feedback gives the system negative stiffness and causes toggle action, which is the opposite of self-centering behaviour. By adjustment of the gain of the position feedback, known amounts of stiffness could be added to, or subtracted from, the system. The equation that is used to calculate the original stiffness and inertia is derived below.

<u>Calculation of inertia of wrist by addition of known inertia to resonating system.</u>

Fo = original resonant frequency

Fb = resonant frequency when bar is added

Jo = inertia of wrist

K = stiffness of wrist

Jb = inertia of added bar

$$Fo = \frac{1}{2\pi}\sqrt{\frac{K}{Jo}} \qquad -(1)$$

$$Jo = \frac{K}{(Fo\ 2\pi)^2}$$

$$Jo + Jb = \frac{K}{(Fb\ 2\pi)^2}$$

$$\therefore \quad Jb = \frac{K}{(Fb\ 2\pi)^2} - \frac{K}{(Fo\ 2\pi)^2}$$

$$= K \quad \frac{1}{(Fb\ 2\pi)^2} - \frac{1}{(Fo\ 2\pi)^2}$$

$$= K \quad \frac{Fo^2 - Fb^2}{(Fb\ 2\pi)^2 Fo^2}$$

$$\therefore \quad K = \frac{Jb}{\dfrac{Fo^2 - Fb^2}{Fb^2 Fo^2 4\pi^2}}$$

$$= \frac{4Fo^2 Fb^2 \pi^2 \; Jb}{Fo^2 - Fb^2}$$

$$Jo = \frac{K}{Fo^2 4\pi^2}$$

$$= \frac{\frac{4Fo^2 Fb^2 \pi^2 \; Jb}{Fo^2 - Fb^2}}{Fo^2 \; 4\pi^2}$$

$$= \frac{Jb \; (Fb)^2}{(Fo)^2 - (Fb)^2}$$

This equation gives the inertia of the hand, and this value can be inserted in equation (1) to calculate the wrist stiffness (Ko). Alternatively, stiffness can be directly calculated by a known alteration to K. Negative position feedback can be used to increase the stiffness by a factor Kf; the new resonant frequency Ff is higher than Fo. With positive position feedback Kf is negative and Ff is lower than Fo. By a calculation similar to the above, it can be shown that:

$$Ko = Kf \; \frac{(Fo)^2}{(Ff)^2 - (Fo)^2}$$

Again, if the stiffness is thus calculated, the inertia can be derived from equation (1). For sensible results, care must be taken to ensure that the limb is operating in its linear region. With positive position feedback the toggle action (negative stiffness) must be less than Ko or the system is no longer resonant. For accurate results it is desirable to correct for the inertia of the apparatus (0.6 g. m^2). The accuracy of this method was tested by using the mechanical model described earlier. Its stiffness and inertia were calculated by adding 5.0 g. m^2 of inertia to the system, by decreasing the stiffness of the system by 0.3 N m rad^{-1}, or by increasing the stiffness by 1.4 N m rad^{-1}. The inertia of the apparatus was corrected for. The results are listed in table (3.8).

The known inertia of the model (determined by calculation) was 5.0 g. m^2, and its stiffness (determined by static measurement) was 1.25 N m rad^{-1}. These methods yield results which are reasonably consistent, and the values are within 10% of the actual values. As the additional inertia method was simplest to use in practice, it was employed on the majority of occasions.

The stiffness and inertia of eight male subjects and four female subjects were determined using this method. Both wrists were investigated. A typical result is shown in fig (3.19). The torque employed in all these measurements was 0.30 N m; at this level the wrist operates as a linear system (fig 3.10). In all the subjects resonant frequency was determined by swept sine wave analysis, although positive velocity feedback could have been used. A control resonance was obtained, and the experiment repeated with 5.0 g. m^2 additional inertia. The results are summarised in table (3.9).

The resonant frequencies (Fo) ranged between 2.1 and 2.8 Hz. The calculated range of inertia (Jo) varied from 2.3 g. m^2 to 4.9 g. m^2. All the subjects were right handed. The inertia of the left and right wrist of each subject is shown in fig (3.20). The men have generally larger inertia, although there is some overlap. There is no obvious trend in the relative inertia of the right and left limb; most values are quite well matched, but one male subject (B.M.) has an inertia of the right wrist that is clearly much larger than that of the left.

The corresponding stiffness measurements are shown in fig (3.21). Again the female subjects have generally lower values and in the majority of subjects there is not a great difference between the left

Table 3.8 Inertia and stiffness determination using mechanical model.

	CONTROL	EXTRA INERTIA	DECREASED STIFFNESS	INCREASED STIFFNESS
RESONANT FREQUENCY (Hz)	2.6	1.8	2.3	3.8
INERTIA g. m^2		4.6	5.1	4.6
STIFFNESS N m rad^{-1}		1.23	1.37	1.23

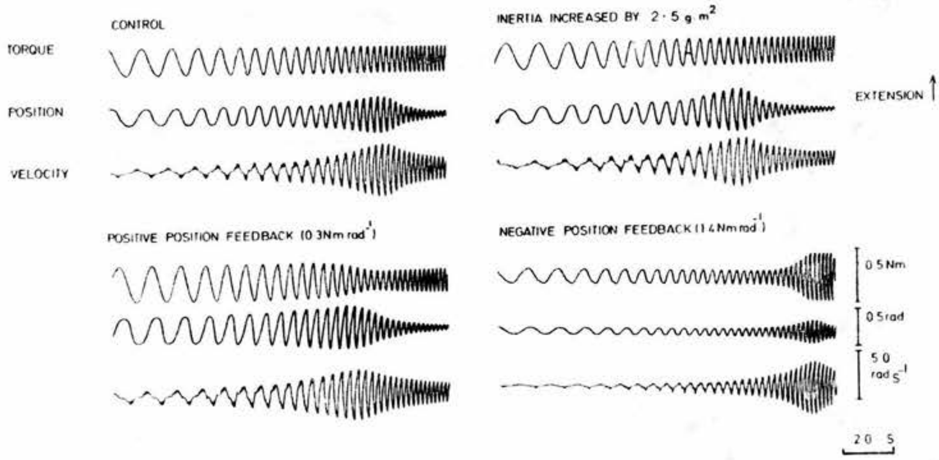


Fig. 3.19 Resonance of the wrist with the addition and subtraction of stiffness, and the addition of inertia. The resonant frequency initially is 2.8 Hz. Added inertia and positive position feedback slow this to 2.2 Hz and 2.4 Hz respectively. Negative position feedback increases resonant frequency to 4.7 Hz. (Subject M.L. 26 m right wrist).

Table 3.9 Inertia (Jo) and stiffness (Ko) of 8 male and 4 female subjects (both wrists)

			LEFT				RIGHT			
NAME	SEX	AGE	Fo (Hz)	Fb (Hz)	Jo (g. m^2)	Ko (N m rad^{-1})	Fo (Hz)	Fb (Hz)	Jo (g. m^2)	Ko (N m rad^{-1})
I.P.	M	21	2.3	1.4	2.94	0.61	2.3	1.4	2.94	0.61
I.C.	M	22	2.0	1.3	3.66	0.57	2.3	1.5	3.71	0.78
A.M.	M	22	2.0	1.3	3.66	0.57	2.9	2.0	4.54	1.50
H.M.	M	21	2.1	1.4	4.00	0.70	2.3	1.4	2.94	0.61
B.M.	M	21	2.8	1.6	2.43	0.75	2.7	1.9	4.90	1.41
T.G.	M	20	2.3	1.4	2.94	0.61	2.1	1.3	3.10	0.54
K.M.	M	21	2.3	1.6	4.69	0.98	2.7	1.8	4.00	1.15
M.L.	M	26	2.4	1.5	3.16	0.72	2.6	2.1	2.34	0.93
A.L.	F	23	2.3	1.3	2.34	0.49	2.8	1.6	2.43	0.75
D.P.	F	20	2.2	1.1	1.67	0.32	2.5	1.3	1.85	0.46
I.S.	F	45	2.5	1.2	1.49	0.37	2.5	1.3	1.85	0.46
S.P.	F	36	2.7	1.6	2.70	0.78	2.3	1.3	2.34	0.49

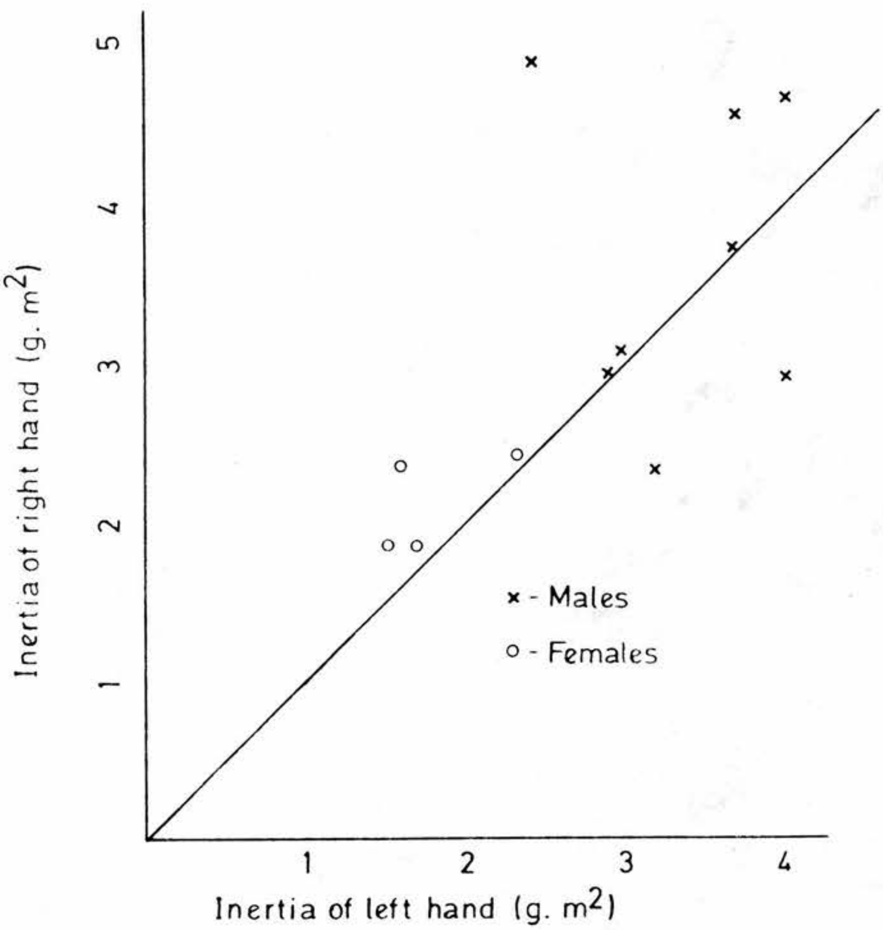


Fig. 3.20 Inertia measurements. The calculated inertia of the left and right hand of 8 male and 4 female subjects is shown. The majority of subjects have quite similar values for both wrists; one male subject has an inertia of the right wrist that is nearly double that of the left. The women have generally smaller inertia than the me n, but one male subject has an anomalously low value for his right wrist.

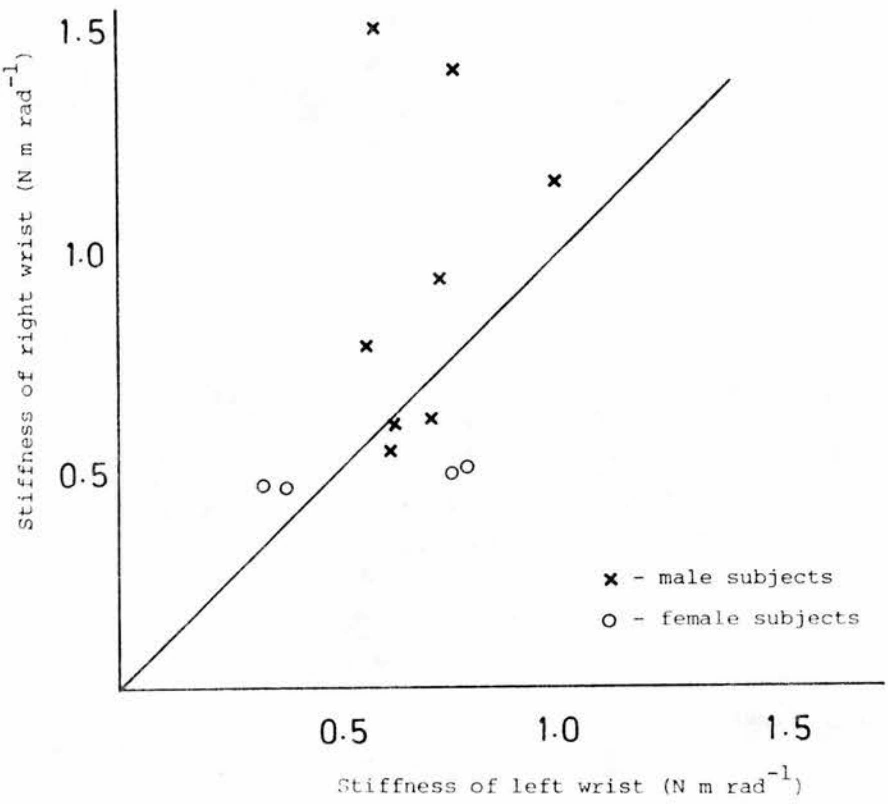


Fig. 3.21 Stiffness measurements. The calculated stiffness of the left and right wrist of 8 male and 4 female subjects is shown. The majority of subjects have quite similar values for both wrists; 2 men have right wrists that are considerably stiffer than their left wrists. The men have generally stiffer wrists than the women, but there is some overlap.

and right wrists. Two male subjects, however, have a clearly greater stiffness of the right wrist.

The significance of these results is uncertain. Clearly, the inertia and stiffness of the joint are complex parameters which depend on a number of factors, such as muscle bulk, joint friction, tissue surrounding the joint, etc. Other more subtle factors involving the "fitness" of the subject may also be important.

The difference between subjects can be explained by qualitative or quantitative differences between them. The bulk of the available evidence points to it being a quantitative difference. The stiffness of a healthy joint is determined by the amount of muscle that must be stretched; on this basis the results suggest that the majority of male subjects have a larger muscle mass than female subjects. Direct confirmation of this is difficult because of the complicating effect of differing amounts of sub-cutaneous tissue.

Cormack and Lamb (1981) plotted the strength of the grip against forearm circumference for a number of subjects. Two parallel lines were obtained, one for men and one for women. The gradient of these lines was identical. There was some overlap between the sexes, but males generally had greater grip strength and larger forearms. They were able to explain the horizontal distance between the lines as a distortion caused by the presence of larger amounts of sub-cutaneous fat in female subjects. They concluded that apart from this: "identical physiological relationships hold in both sexes: men are stronger because they have larger muscles".

Other investigators, who have measured joint stiffness, have found similar sex differences. Such et al. (1975) measured peak to peak values and energy dissipation of hysteresis loops obtained under the application of sinusoidal displacements to the knee, and showed that the average energy loss of the female group was 54% of the males.

Wright and Johns (1960) and Backlund and Tiselius (1967) measured the stiffness of the metacarpal phalangeal joint, and demonstrated that the measurement in females was approximately 60% of that in males.

Thompson (1978) found that the resistive torque encountered on passively moving the knee joint was approximately 50% lower in female than male subjects. He attempted to correlate these stiffness values with the following parameters: body weight, girth of the thigh, and strength of the thigh muscles. He found that the best correlation was between the muscle strength and joint stiffness, and suggested that this indicated: "that it is muscle bulk rather than fatty tissue that is the dominant factor in determining the stiffness characteristic". He concluded that the sex difference could be explained on purely anthropometric grounds.

It therefore seems likely that these anthropometric differences can explain the generally smaller stiffness of the female subjects.

The interpretation of the inertia results is less straightforward. Inertia increases linearly with mass and as the square of the radius of gyration. Small increases in the size of the hand might be expected to cause larger increases in inertia than relatively larger increases in mass; size and shape are more important than mass. Similarly, differences in the mechanical advantage of the coupling of muscles to the skeleton will have an influence on inertia.

It would be expected that, in view of the greater muscle mass and larger skeleton, the inertia of the body segments of male subjects would be larger than those of female subjects. This seems to be confirmed by the results; the men investigated had generally larger calculated values of inertia than the women, although one male subject had an inertia of the right wrist that overlapped the female group. The discovery that female subjects have smaller inertia and less stiffness explains why the resonant frequency of male and female subjects is not significantly different at high torque levels.

It is noteworthy that considerable tension is generated on passively moving the wrist. If the tendons exert their force approximately 1.5 cm from the axis of the joint, and the stiffness is 1.0 N m rad^{-1}, a displacement of 1 rad (57.3^{o}) of the hand gives rise to a force in the stretched muscle of about 67 N (approximately 7 Kg f). Although this seems a large amount of force, it is relatively insignificant compared to the force exerted by the active muscles.

If a hand-held lever 1 m long is employed to exert a force caused by voluntary maximal flexion of the wrist joint, the torque generated is approximately 40 N m (our data using one male subject). Assuming the same radius of action of 1.5 cm, this suggests that the active tension in the flexor muscles is approximately 2700 N (270 Kg f). Thus the passive tension is equal to only 1.5% of the maximal active tension.

3.2)9 Low amplitude sinusoidal analysis.

If the wrist is considered as a torsional pendulum system, application of a sinusoidal torque input will produce a sinusoidal displacement at the same frequency. The amplitude of oscillation will be controlled by the size of the applied force, the relationship of the applied frequency to the resonant frequency of the system, and the damping in the system. There will be a difference in phase between the applied torque waveform and the resulting velocity; this will be 0^{o} when the applied frequency is equal to the natural resonant frequency of the system.

Thus, when a small sinusoidal torque at 3.0 Hz ("driving force") is applied to the relaxed wrist, a displacement at the same frequency, but shifted in phase, is observed (fig 3.22). This figure also shows the effect of applying a transient larger perturbation to the system. A square wave torque of the same frequency but three times larger is applied at A. This "stirring force" is automatically locked in frequency and phase onto the smaller driving force; a zero-crossing detector ensures that the transition from one to another is smoothly accomplished. The stirring force can be applied for any desired number of cycles, in this case three. When the stirring force is removed and the force reverts to its previous lower level, the displacement of the hand is considerably greater than it was previously for the same torque input; clearly the ratio of the resonant frequency to the driving frequency, or the damping, or both, has been changed by the application of the stirring force. This is not a transient phenomenon; it persists as long as the system is kept in motion.

If the driving force is cut for three cycles (B), or four cycles (H) the system reverts to its previous original amplitude when the force is reapplied. Two cycles of stirring force (C) and one cycle of stirring force (E) produce the same large increase in amplitude. When the force is cut for less than three cycles (at D, F and G), the amplitude decreases to an intermediate value. A stirring force that has a sinusoidal or triangular waveform is equally effective. Active movements of the subject also serve to increase the displacement.

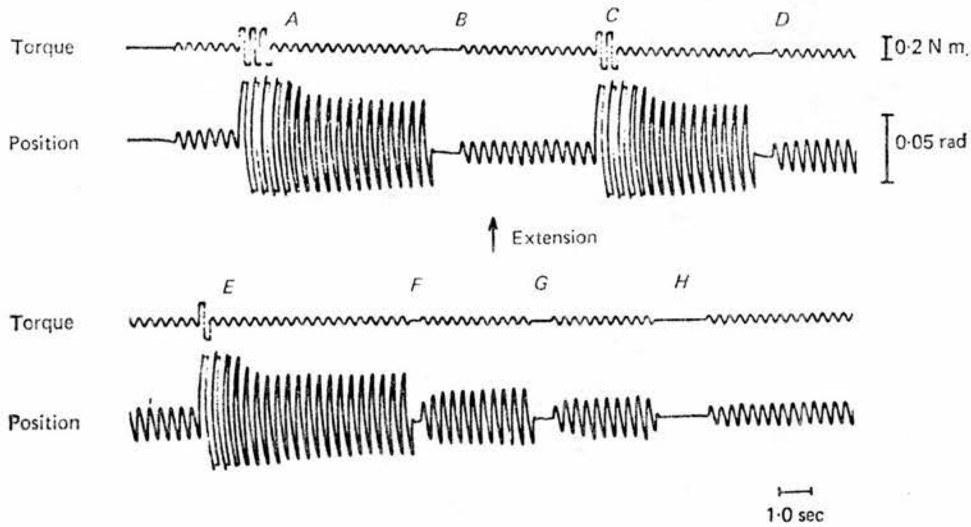


Fig. 3.22 "Postural thixotropy". The effect of a "stirring force" on the response of the wrist to a small sinusoidal driving force at 3.0 Hz is shown. At "A", "C", and "E" a perturbation of 3, 2 and 1 cycle cause the same increase in amplitude. At "B", "D", "F", "G" and "H" the driving force is cut for 3, 2, 1, 2 and 4 cycles respectively. 3 or 4 ("B" and "H") cycles cause a reduction in amplitude to the original level; less than 3 cycles ("D", "F" and "G") cause a partial reduction. All changes can be prolonged indefinitely. (Subject F.C. 25 m right wrist).

Stirring forces much smaller than those shown are not effective in increasing the amplitude. The stirring force is not particularly critical in respect of frequency or waveform, although it requires to be adequately large to elicit the effect. However, the driving force and frequency must be held within relatively narrow limits.

This type of behaviour demonstrates that the postural system meets applied forces with a resistance that is dependent on its previous history of movement. We have named this property postural thixotropy (Lakie, Walsh and Wright, 1980).

"Driving" force

It is impossible by this method to determine an exact threshold value of driving torque above which the effect is seen and below which it disappears. This is because the value of torque depends very critically upon the frequency that is employed; a torque that may elicit an effect at one frequency may not do so at another. Another difficulty is that the effect is not all or nothing; a small driving torque may give rise to a small increase in displacement after the system is stirred, but a slightly larger driving torque may give a much larger displacement after the same amount of stirring. Also, a small driving torque may give an increased displacement after a great deal of stirring, but fail to do so after a lesser amount of stirring.

These constraints imply that considerable care must be taken in interpreting the data from these experiments, and only simple inferences can be drawn from the results. The experiment is nevertheless a striking and convincing demonstration of the non-linear properties of the musculature.

With driving torques greater than approximately 0.25 N m at the wrist, no increase in amplitude is observed after vigorous stirring. Such torques presumably maintain the system in a stirred condition; thus an increase in displacement following even the largest perturbations is not possible. Conversely, with forces that are much smaller than 0.1 N m a transient increase in amplitude may be observed following stirring; the force is presumably too small to maintain the muscles in a stirred condition. An illustration of this type of transient increase with a very small driving torque is shown in fig (3.23). Between these upper and lower limits lies the range of driving torques which will demonstrate the effect.

With torques that border on the upper limit, the amplitude of oscillation sometimes increases spontaneously over a period of a few seconds; evidently the driving force is itself just sufficient to stir the system. Similar "growth" in the response of an ankle oscillating near resonance has been reported by Agarwal and Gottlieb (1977).

It is significant that the range of torques in which this behaviour occurs is about 0.1 N m to 0.25 N m, which is the region in which the postural system of the wrist becomes highly non-linear in stiffness and damping. It now appears that this non-linear behaviour is dependent on the prior history of movement of the limb.

The frequency of the driving force is also rather critical. The thixotropic effect is most pronounced when the driving frequency is near the frequency at which the limb resonates in its linear region. This relationship between size of response and driving frequency is shown in fig (3.24).

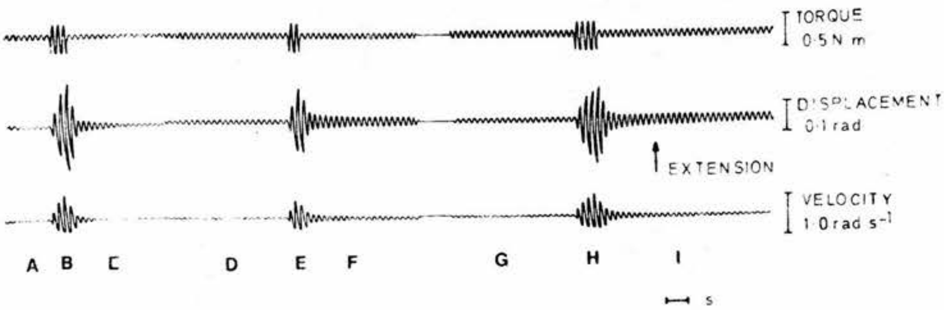


Fig. 3.23 "Driving force" and "stirring force". At "A" a small sinusoidal force (driving force) at 3.0 Hz is applied to the wrist. "Stirring" with a sinusoidal force of 4 times the size "B" causes a transient increase in amplitude "C". Increasing the size of the driving force slightly "D" gives a sustained increase in amplitude "F", even though the stirring force "E" is only applied for 2 cycles.

When the driving force is further increased "G" and the stirring force applied for a longer time "H" the resulting increase in amplitude "I" is no greater than that observed at "F". This illustrates the critical nature of the driving force. (Subject D.L. 42 m right wrist).

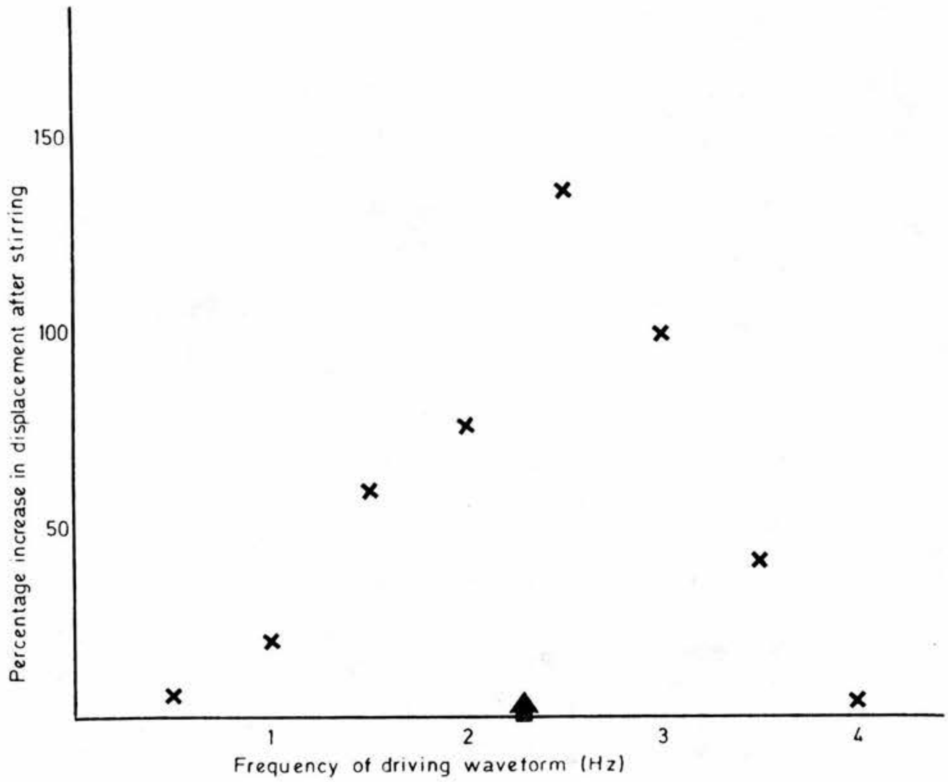


Fig. 3.24 Influence of frequency on "thixotropic" response. The percentage increase in amplitude following the application of 4 or 5 cycles of square wave stirring torque at 0.4 N m. The driving torque was held constant at 0.08 N m. These results would have been different if the driving force had been adjusted to maximise the effect at each frequency. The resonant frequency is indicated by an arrow.
(Subject D.L. 42 m right wrist).

If stirring decreases the stiffness of the wrist it will lower its resonant frequency, and thus the driving frequency may now coincide with the resonant frequency of the system, producing a much larger displacement. Driving frequencies that are higher than the resonant frequency show the effect poorly or not at all. The effect is, however, just evident with lower frequencies; it appears for example if small square waves with a frequency of less than 1 Hz are employed.

"Stirring" force

The size of the stirring waveform is much less critical than the size of the driving waveform. Very small stirring forces are ineffective, and do not produce an increase in amplitude, or may produce a slight increase, or one that is transient. Large stirring waveforms produce a large increase in amplitude, but no further increase in size is caused by employing an even larger stirring force. Between these two limits lies the range which causes a variable increase in size. The response is not all or nothing; small stirring forces may produce a smaller increase in displacement than large ones. Usually, these small increases will spontaneously "grow" and the response will ultimately reach the same size as that produced more directly by the application of a larger stirring force.

Similarly, there is no precisely definable minimum time for stirring to be effective. A stirring force that is apparently inadequate may suffice if it is applied for a longer time. A stirring force which will just evoke a response on some occasions may fail to do so on others. Square waves, in which the acceleration and velocity are maximal, appear to be the most effective form of stirring force; slow sinusoidal movements are less effective.

Very small voluntary or passively imposed movements act as an effective stirring force, gentle isometric contractions tend to be inadequate. It thus appears likely that the effect is linked to a critical velocity. This was investigated using ramped positive velocity feedback (section 3.2)11).

3.2)10 Neuromuscular blockade.

The thixotropic effect was most obvious at a frequency of under 3 Hz; this suggested that it might be a voluntary or semi-voluntary response of the subject. This was investigated in five anaesthetised patients. Clear thixotropic changes were observed following the induction of anaesthesia, and the administration of neuromuscular blocking drugs. It is not possible to be sure that neuromuscular blockade is effective at all neuromuscular junctions, but when stimuli were applied to the ulnar and median nerves with a clinical stimulator, no muscular twitching was observed. Furthermore, at no time during the experiments was EMG activity from the flexor and extensor muscles detected, and this makes it extremely unlikely that the effect is neurally mediated.

With unconscious anaesthetised patients thixotropic changes could be monitored conveniently over long periods of time; fig (3.25) shows the record from one such patient where the increased amplitude was still evident after more than 1.5 minutes had elapsed. Similar long term thixotropic changes have been observed regularly in the spastic wrist and elbow of hemiplegic patients, some of whom had no power of voluntary movement in the extremity tested.

Postural thixotropy cannot therefore be a voluntary response of the subject, its persistence in unconscious subjects following neuro-muscular blockade, and the absence of EMG activity make it very

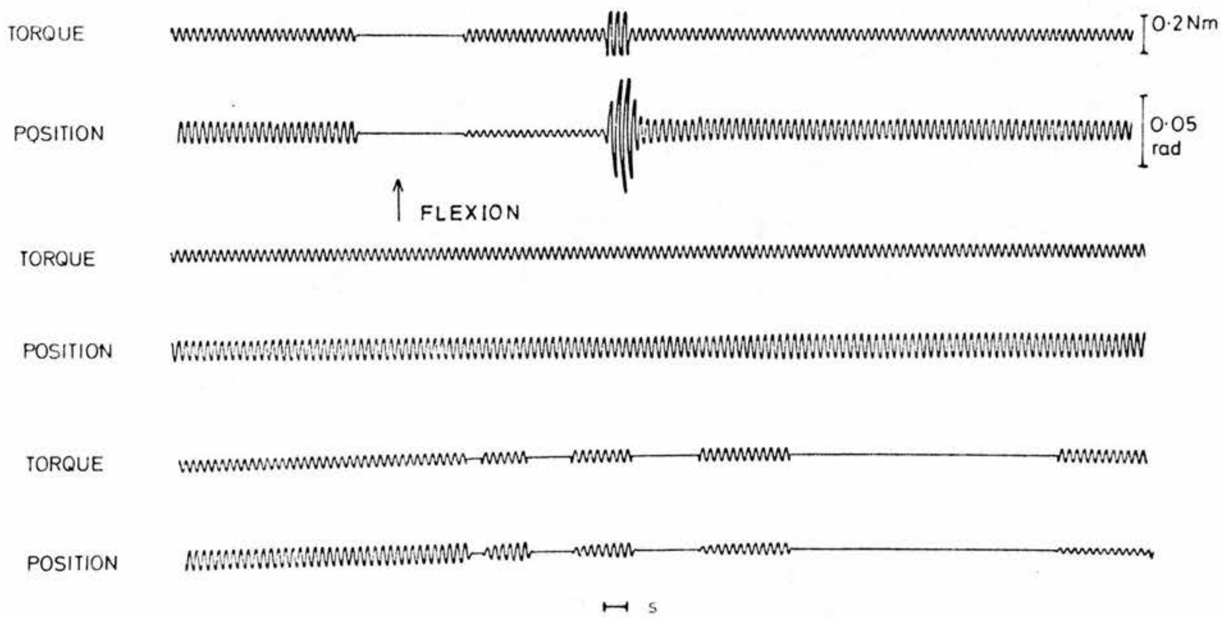


Fig. 3.25 Thixotropic changes in an anaesthetised subject. This record was obtained from an anaesthetised subject approximately 30 s after the i.v. administration of 35 mg suxamethonium. The increase in amplitude after the application of a stirring force persists indefinitely; the amplitude returns to its original level when the driving force is cut for more than 2 or 3 seconds. (Subject G.U. 42 m left wrist. Laminectomy).

unlikely that it is a neurally mediated effect, and it presumably arises as a consequence of the mechanical properties of resting skeletal muscle.

Thixotropic changes of the same type were also observed in normal subjects at the elbow, ankle, knee, jaw, and the distal and middle phalanges of the index and middle finger. Pronation and supination movements of the wrist also showed thixotropy. In fact, thixotropy has so far been seen whenever a muscle or muscles are moved, so long as the driving torque is not too large, and the frequency is similar to the frequency at which the limb resonates with large torques. Thixotropic changes have not been observed when the muscles are voluntarily isometrically contracted; it may be that thixotropy is not a property of active muscle, or alternatively the force required to elicit it may be outwith the range of the apparatus.

3.2)11 Ramped positive velocity feedback.

The effect of applying negative damping to the wrist has been described previously. In this series of experiments the feedback generated torque was automatically linearly increased and decreased, reaching a maximum every ten seconds. The force reached a minimum level of 0.01 N m rather than zero, as with zero force the motion stopped and would not always spontaneously restart, thus causing a gap in the record.

A frequency meter was employed to plot the instantaneous value of frequency, and the output of the frequency meter was squared by an analogue module (Burr-Brown Ltd.) and continuously recorded. The stiffness of the system is proportional to the resonant frequency squared and this record gives a continuous measurement that is proportional to the wrist stiffness. It is possible to calibrate this by the addition of known amounts of inertia, but this was not done in the majority of experiments.

Fig (3.26) shows a typical record produced by ramped positive velocity feedback. With high torques the resonant frequency is constant, the frequency squared record is a plateau, and the stiffness is therefore linear. As the force falls the rate abruptly increases; inspection of the frequency squared record shows that the wrist is at least twice as stiff. The displacement and velocity records also show evidence of linear damping for larger forces; the displacement and velocity maxima increase linearly with torque. This linear relationship does not hold for low torque levels when the system is stiff. In this region the system is so heavily damped that the smallest forces produce practically no displacement or velocity.

Considerable asymmetry is evident in all the traces. The linear region persists for much longer as the force is decreasing and the system is being kept in motion, and the stiffness increases as the force wanes much more steeply than it decreases as the force increases. This is clear evidence of the dependence of the compliance of the system on previous movements (thixotropy). The system can "remember its past history of movement". There are therefore two "torque thresholds"; one when the force is increasing and the other for a decreasing force. In fig (3.26) the torque at which the wrist enters its linear region is 0.13 N m as the torque is increasing. This corresponds well with the mean value of torque threshold (0.14 N m) determined for female subjects in the resonant frequency experiments.

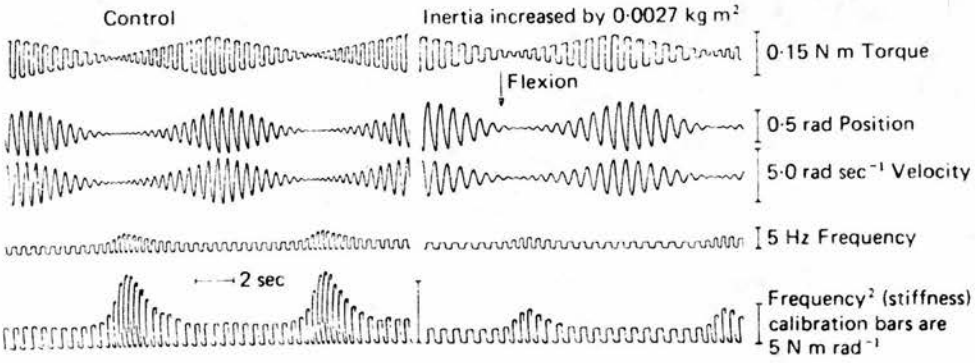


Fig. 3.26 Ramped positive velocity feedback. The interrelationship of torque and resonant frequency is shown. The stiffness of the system is proportional to the frequency squared. The stiffness rises abruptly at a low torque level (0.03 N m) as the force wanes, reaches a maximum which does not coincide with the lowest torque, and decreases gradually as the torque increases. A linear "plateau" of stiffness is reached at a torque of 0.13 N m. This highly asymmetrical behaviour provides evidence of thixotropy in the system. The stiffness record was calibrated by the addition of 2.7 $g.m^2$ inertia.
(Subject M.A.L. 26 f right wrist).

Attempts to show thixotropic behaviour using the mechanical model earlier described have been unsuccessful; it is difficult in any case to see where thixotropy could arise in a torque generator of this type.

3.3 COMPLIANCE MEASUREMENTS

3.3)1 Rectangular waves.

In fig (3.27) an alternating large rectangular torque is applied to the wrist. The hand moves in the direction of the force, reaching a steady level after an overshoot and one or two decrementing oscillations. In a fully relaxed subject these oscillations are more marked in flexion than in extension, and their frequency is approximately 2 Hz - the resonant frequency of the wrist. The velocity with which the hand moves is determined by the damping of the system; the presence of decrementing oscillations shows that it is less than critically damped.

The displacement for a given torque is by definition the compliance of the wrist (the reciprocal of stiffness). If the wrist is voluntarily stiffened, the displacement of the hand is much reduced, and it becomes virtually fixed in the stiffened position. The amplitude of the overshoots is much reduced, and the frequency of the decrementing oscillations is increased proportional to the degree of effort. When large reciprocating forces were applied to the wrists of relaxed subjects, EMG activity was observed. This activity usually took the form of a burst of firing in the muscles that were being shortened; it was generally more evident in the flexor muscles. Phasic stretch reflexes were not seen except when the applied torque was very large or the subject poorly relaxed, and tonic stretch reflexes were never observed in relaxed normal subjects, although they were seen in a number of spastic stroke patients. When normal subjects voluntarily slightly stiffened the wrist by co-contraction, prolonged firing during stretch, corresponding to a tonic stretch reflex, was observed.

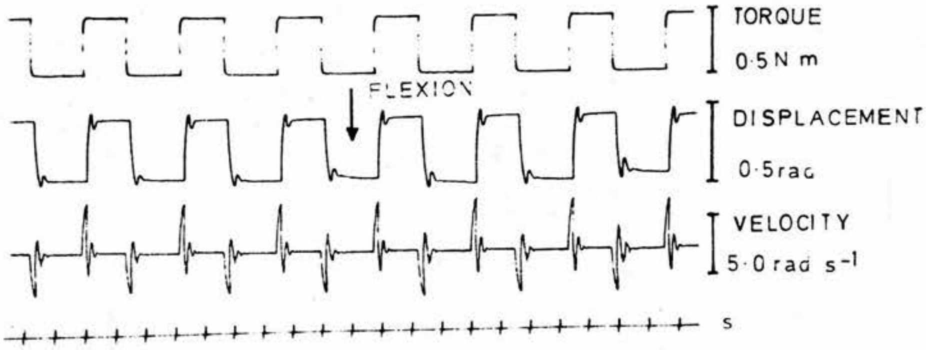
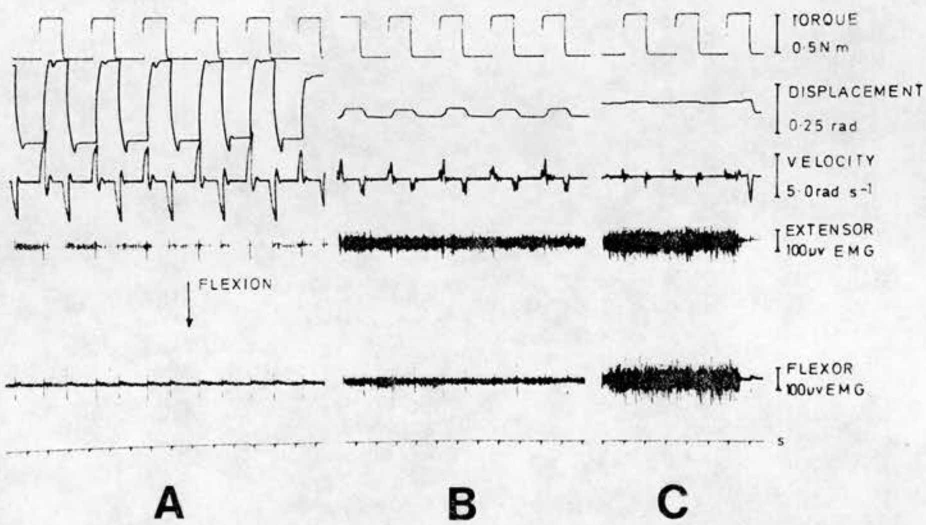


Fig. 3.27 Rectangular torque pulses. An alternating rectangular torque is applied to the wrist. The wrist follows the applied torque; overshoots and decrementing oscillations are seen in the displacement record. The wrist is evidently less than critically damped. The velocity with which the wrist moves is determined by its viscous resistance.
(Subject G.W.E. 45 m right wrist).

Joint compliance, defined as the ratio of displacement to applied torque, reflects changes in muscle tone. A normally relaxed joint moves easily and has high compliance, whereas the compliance of a tense or rigid limb is low. It was possible to demonstrate a clear reciprocal relationship between the compliance and the EMG (fig 3.28). It might appear that this is a simpler and more direct method than resonant frequency analysis for the measurement of muscle tone. In theory this is certainly true, but in practice it suffers from the serious disadvantage that it is necessarily performed using a low frequency rectangular wave, and it is possible for the subject to predict where the next torque reversal will occur and thus aid or interfere with the motion. On several occasions movement has been seen to continue after the motor was switched off! This is a serious disadvantage. It can to some extent be overcome by using rectangular waves of random repetition frequency but many subjects still find it difficult not to interfere with the motion. Not surprisingly, compliance measurements made by this method show poor long and short term reproducibility.

Some measurements were made on hemiplegic patients using this method. One female patient had both wrists tested on 4 consecutive days. The spastic wrist, which had no apparent voluntary movement, was very stiff (0.7 rad N m^{-1}) and reproducibility was good: the other wrist, which appeared to be normal, varied between 1.4-3.2 rad N m^{-1} on day one, 2.0-3.2 rad N m^{-1} on day two, 2.3-3.0 rad N m^{-1} on day three, and 1.9-3.6 rad N m^{-1} on the final day. Thus this technique is not well suited to the accurate measurement of muscle tone in normal



<u>Fig. 3.28</u> Relationship between EMG and wrist compliance. At "A" the wrist is relaxed, it has a high compliance, and overshoot and decrementing oscillations are seen. "Shortening" reactions are seen in the extensor trace. At "B", the wrist is stiffened by voluntary co-contraction and the compliance is reduced to about one eighth of its previous value. At "C" the wrist is maximally stiff and the compliance is reduced to practically zero. An oscillation at approximately 8 Hz can be discerned in the velocity trace when the force reverses.
(Subject G.W.W. 45 m right wrist).

conscious subjects. The compliance of the wrist in 10 normal relaxed subjects, determined by this method is shown in table (3.10). Because of the variability of this method, no attempt was made to demonstrate a difference between male and female wrists.

Two further serious problems stem from the highly non-linear properties of the musculature. Small forces produce virtually no displacement and large forces produce disproportionally large movements. The compliance is also dependent on the prior history of movement of the muscles.

3.3) 2 Ramped rectangular waves and composite compliance curves.

This method was employed to investigate the non-linear behaviour of the wrist and other joints. A series of ramped rectangular torque pulses was applied to the joint and the resulting displacement recorded. The torque reversed at approximately 1Hz; the pattern of displacement is shown in fig (3.29). Inspection of this record shows that whereas the torque rises in linear steps, the displacement trace is decidedly non-linear. Three phases can be distinguished as the torque increases. At first, the compliance of the system is very low, the first five or six torque pulses produce a minimal displacement. In this region the wrist is evidently heavily damped; overshoots are not seen. The second phase commences at a torque level of approximately 0.25 N m. In this region the displacement of the wrist starts to increase rapidly, and overshoots are observed; the damping has decreased.

This transition region, in which the stiffness and damping decrease, is followed by the third phase in which the compliance is initially approximately linear; increases in torque cause

Table 3.10 Compliance of the wrist of 10 subjects using rectangular torques at 0.5 Hz

Subject	Age (yr)	Sex	Wrist	Torque (N m)	Compliance (rad N m^{-1})
S.T.	32	M	R	0.7	1.34
P.B.	24	M	R	0.6	0.61
J.W.	23	F	R	0.6	2.39
P.H.	21	M	R	0.6	1.67
			L	0.5	1.87
G.F.	24	M	L	0.6	3.30
G.W.	18	F	L	0.6	2.87
			R	0.6	2.88
G.W.	45	M	R	0.7	3.14
			L	0.5	3.04
S.P.	26	F	L	0.6	2.00
			R	0.4	2.22
M.McC.	19	F	L	0.5	0.88
M.L.	25	M	R	0.7	1.20
			L	0.6	1.11
				Mean	2.06
				s.d.	0.84

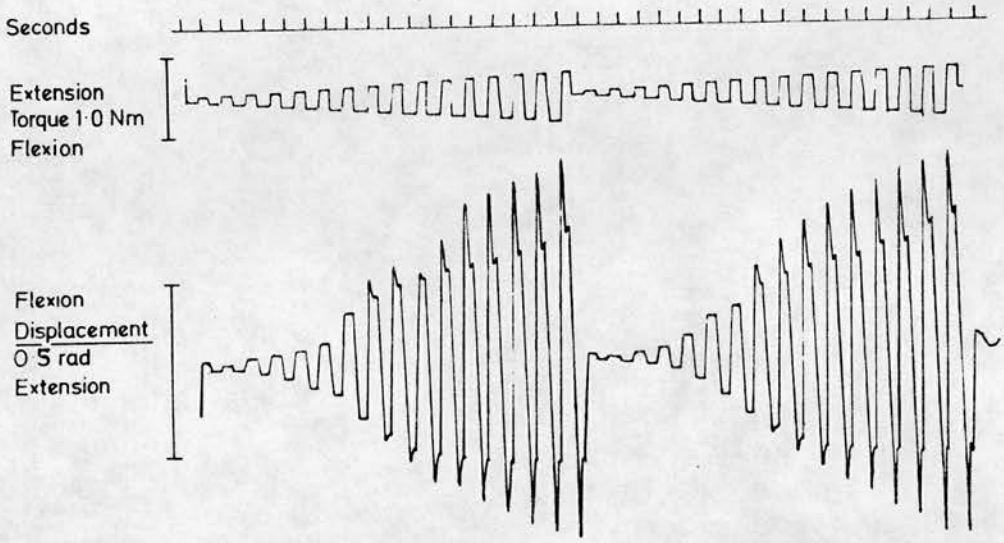


Fig. 3.29 Ramped rectangular torques. A linearly increasing series of torque pulses is applied to the relaxed wrist. The compliance is non-linear; the first 4 or 5 torque impulses produce a disproportionally small displacement. The compliance then increases rapidly, and finally begins to decrease gradually. The system is evidently heavily damped for small displacements; overshoots are not seen when the torque is small. (Subject C.E.H. 22 f left wrist).

pro-rata increases in displacement. As the torque rises further the displacement becomes proportionally less; this decrease in compliance is presumably a reflection of the well known tension-length curve of skeletal muscle.

In fig (3.29) both torque and displacement are shown as a function of time; in fig (3.30) displacement has been plotted directly against torque, using a X-Y plotter. The curve obtained, which plots one point for each of the 32 torque reversals, is a composite compliance curve for the wrist.

The value of this technique is that it gives a direct picture of the compliance of the wrist. The stiff region is clearly seen, as is the transition to a region of much greater compliance. In this region large overshoots can be seen. The progressive stiffening of the system with the largest torques is also evident.

In fig (3.31) the compliance curves of a male and female subject are compared. The compliance of the female subject is considerably greater; the displacement at all torque levels is larger. This is in agreement with the relative stiffness values of male and female subjects determined by the resonant frequency experiments. As the composite compliance method gave a clear picture of the "stiff region" the effect of altering the resting position of the wrist with superimposed biasing torques was reinvestigated. The results of a typical experiment are shown in fig (3.32). The overall compliance of the wrist is altered slightly by this procedure. When the wrist is biased into extension the compliance for extensor forces is decreased, and when it is biased into flexion the compliance for flexor forces is decreased. This is the type of behaviour that would be

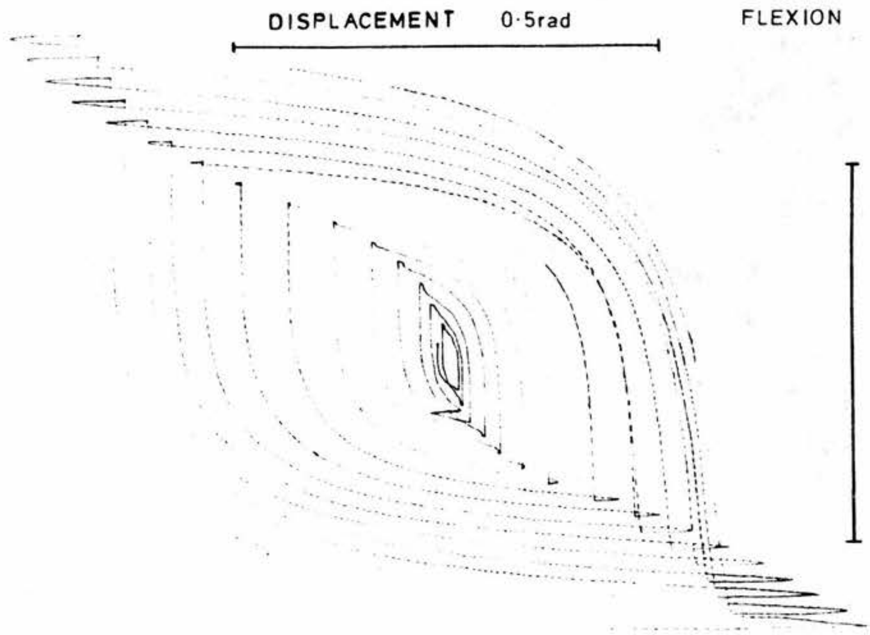


Fig. 3.30 Composite compliance curve of the wrist. Torque vs displacement has been plotted using a X-Y recorder. One point is plotted for each torque reversal. This gives a complete picture of the non-linear stiffness of the wrist; the stiff region is obvious, as is the region of increased compliance and finally the region of increasing stiffness for the largest torques. Overshoots are seen with the largest torque pulses.
(Subject D.M. 25 f left wrist).

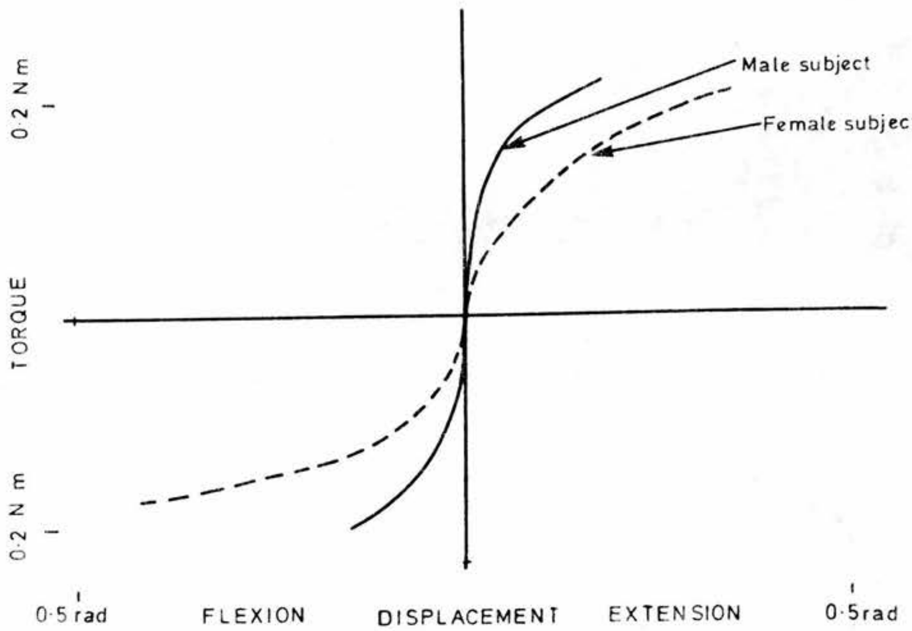


Fig. 3.31 Compliance of a male and female subject, traced from composite compliance curves. The displacement of the female subject is greater at all levels of torque and the size of the stiff region is smaller.

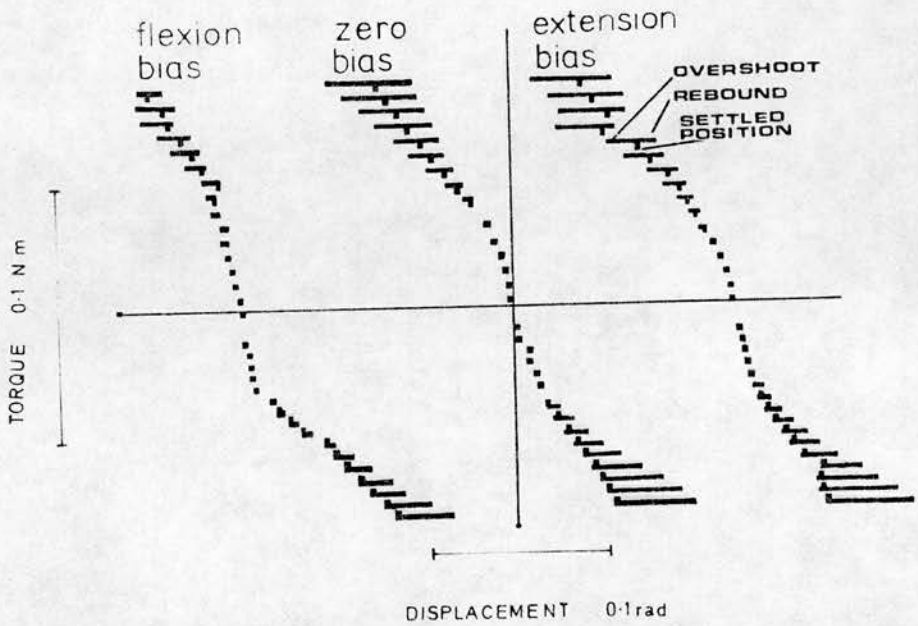


Fig. 3.32 Composite compliance curves with bias. With zero bias the motion of the wrist takes place about its natural resting place; the stiff, highly damped, region can be seen. When additional torques are applied to bias the resting position of the wrist into flexion or extension the size and position of the stiff region are unchanged. It cannot therefore be due to the anatomical features of the wrist. Biasing into flexion decreases compliance in the flexion direction, and biasing into extension decreases compliance in the extension direction.
(Subject F.M. 19 m right wrist).

expected as the wrist is moved closer to its anatomical limits; with greater amounts of bias these changes are more pronounced.

However, no amount of bias alters the size of the stiff region; this is shown clearly in fig (3.32). Thus the stiff region cannot be anatomically determined as it occurs in muscle at different resting lengths. The postural system is stiff about its resting position, regardless of where that resting position happens to be. This "short range stiffness" has been demonstrated by many workers in the isolated muscles of a wide range of animals, under a variety of different names, but has not previously been directly illustrated in the postural system of man.

The compliance results so far described were obtained with biphasic torque inputs; the torque reciprocated from extension to flexion. Different results were obtained when monophasic torque inputs were employed. In this technique the torque impulses acted in only one direction, thus between torque impulses the torque fell to zero. The torque pulses increased linearly in size and then declined linearly and started rising in the opposite direction.

A representative recording is shown in fig (3.33) at A. A very considerable shift in base line can be seen. As the torque declines the wrist ceases to follow individual torque impulses and drifts in the direction of the applied torque. The elastic behaviour of the hand muscles, which were seen at higher torque levels, has been replaced by a viscous response; evidence of highly non-linear properties. This illustrates why it is impossible accurately to measure the compliance of the wrist using single pulses of torque. At one stage a series of pseudorandom monophasic torque impulses were applied to the wrist and the

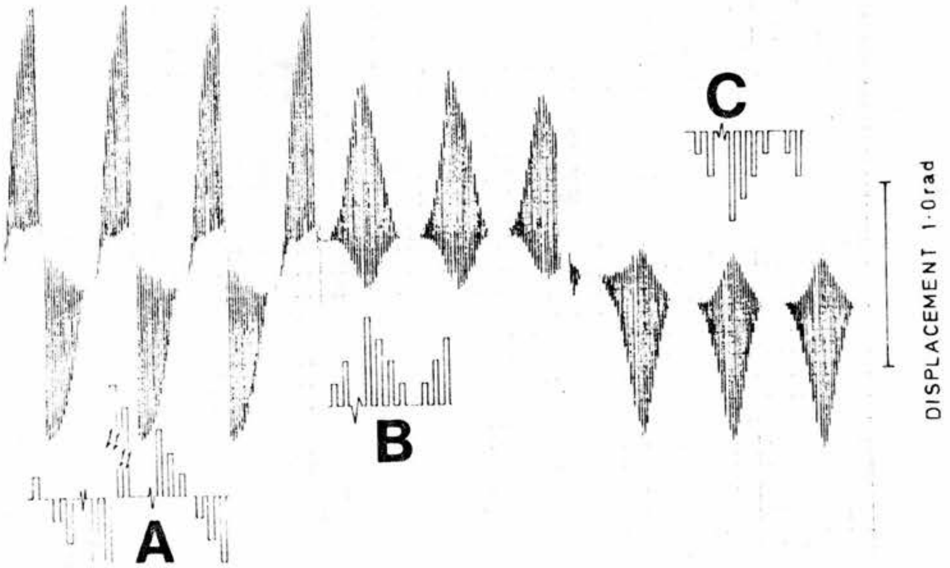


Fig. 3.33 Ramped monophasic torque pulses. In this series of experiments the applied torque did not alternate into flexion and extension, but the torque acted in only one direction, becoming zero between pulses. The displacement only was recorded, but the pattern of applied torque is shown (not to scale).

At "A" the torque pulses linearly increased in one direction, abruptly reversed when they reached their maximum size, and progressively decreased. The resting position of the wrist (base-line) is dependent on the size of the applied torque pulses; with the smallest pulses the wrist does not rebound, but drifts in the direction of the applied torque. This is shown clearly in "B" and "C", where a torque acting only in flexion and extension respectively has been employed. Although the force acting on the wrist between torque pulses is zero in both cases the "base-lines" are considerably different (0.3 rad).
(Subject M.L. 26 m right wrist).

resulting displacement measured. Torque was plotted against displacement in an attempt to construct a composite compliance curve, but the result bore no resemblance to fig (3.30): the reason for this is that the baseline from which displacement measurements are made is not fixed but is dictated to a large extent by the size of the preceding torque impulses. Thus the wrist can "add" several small torque impulses to produce the same displacement as one larger one.

This behaviour of the baseline is shown clearly in fig. (3.33) at B and C. At B the torque pulses are acting in the flexion direction only and the wrist establishes a baseline which stays very constant. However, when the torque pulses are reversed, to operate in the extension direction, the baseline shifts approximately 0.3 rad. It is important to note that no bias is operating - the force acting on the wrist between the torque impulses is zero. Despite this the wrist has altered its position by a considerable amount. Viscous flow (creep) has occurred.

Composite compliance measurements were made before and after anaesthesia in four patients undergoing elective surgery. There was no significant difference between the compliance found before anaesthesia, after anaesthesia, or following neuromuscular blockade in three subjects. One subject had a slightly higher compliance following anaesthesia, but there was no further increase following neuromuscular blockade.

Some measurements of compliance were made in volunteer subjects at the elbow, knee, ankle and finger. Only a few subjects were investigated, and no attempt was made to examine the variability of the results. Each joint investigated showed a similar pattern of non-linearity: the joint was always stiffer for small levels of torque.

To test the linearity of the apparatus, the same model that was employed in the resonant frequency experiments were used. The result is shown in fig (3.34). The response was linear down to 0.05 N m. The compliance of the model does not pass through the origin; this distortion is caused by static friction in the motor. The pattern is, in fact, similar to that seen with a limb, but the static friction of a limb is an order of magnitude greater. Furthermore, this curve was obtained using the G9M4 motor; the G6M4 motor, which was also used in compliance measurements, has a static friction that is smaller. It can safely be concluded that the non-linearities seen in the compliance of limbs are not artifacts of the measuring system.

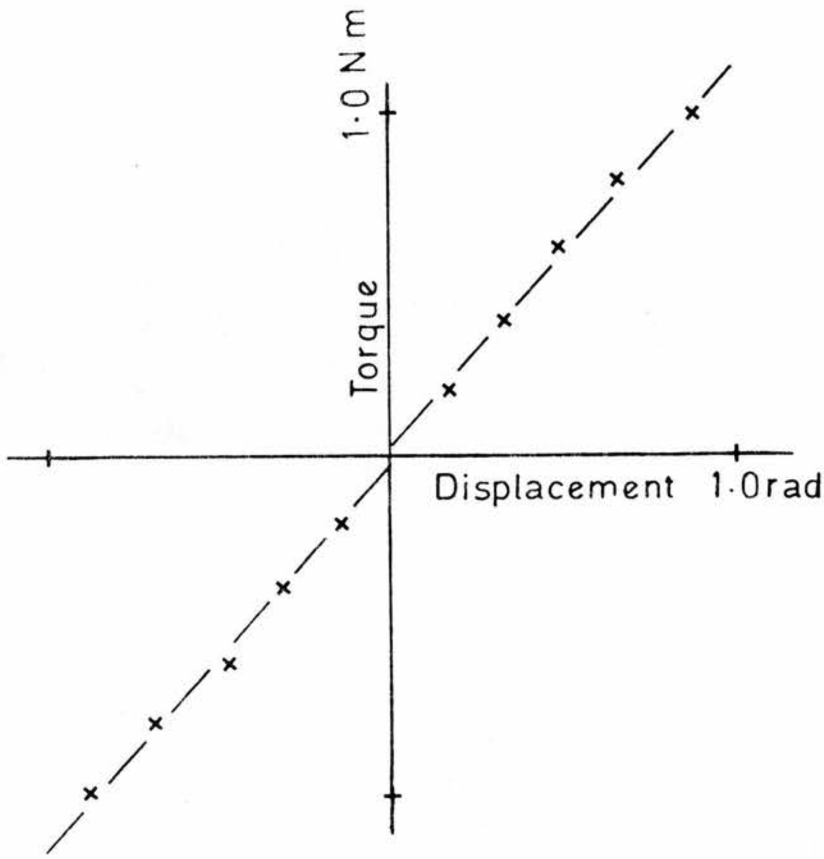


Fig. 3.34 Compliance of mechanical model. The compliance is linear and has a value of 1.25 N m rad^{-1}. The compliance line does not, however, pass through the origin; 0.05 N m torque is required to produce a displacement. This is due to static friction in the motor (G9M4).

3.4 COOLING OF THE MUSCLES

3.4)1 Resonant frequency.

The effect of muscular cooling on the resonant frequency of the wrist was investigated in a number of subjects. Twelve subjects (8 female) had the muscles of the forearm cooled by immersion of the hand and forearm in water at 7-8°C for 10-15 minutes. Measurements of resonant frequency were made before and after cooling using swept sinusoidal waveforms at a torque of 0.35 N m. The results are summarised in table (3.11). In five cases there was no measurable change in resonant frequency, in six there was a slight increase, and in one a decrease. Five subjects cooled only the hand and wrist joint and this procedure did not alter resonant frequency. As a control, three subjects cooled only the hand and forearm of the opposite limb; this did not cause any changes in the limb under test.

Additionally, four different male subjects were tested at different torque levels using continuous cooling. The forearm was enclosed in a water bath which initially contained water at 35°C. During the experiment this water was replaced by water cooled to 4-5°C, and this temperature was maintained for 30-40 minutes. At the end of this time the limb was rewarmed using water at 40°C. Resonant frequency was continuously monitored using swept sine waves and EMG activity was recorded on two occasions with fine wires in the flexor and extensor muscles. Plots of resonant frequency vs. torque were prepared for control measurements after 30 minutes of cooling.

Fig (3.35) shows the pattern of non-linearity of a typical subject before and after cooling. There is no significant

Table 3.11 The effect of cooling the forearm muscles on wrist resonant frequency.

Subject	Age (yr)	Sex	Wrist	Control Resonant Frequency (Hz)	Cooled Resonant Frequency (Hz)
B.E.	19	F	L	1.9	1.9
S.C.	19	F	L	2.3	2.0
A.O.	20	F	R	2.3	2.5
J.C.	19	F	R	2.0	2.3
P.T.	19	F	R	2.5	2.5
C.P.	20	F	R	2.4	2.8
K.F.	19	F	L	2.8	2.8
J.S.	20	F	L	2.2	2.2
M.P.	19	M	R	2.1	2.5
S.G.	19	M	R	2.6	2.7
I.G.	22	M	L	2.0	2.1
K.F.	20	M	R	2.5	2.5
			Mean	2.3	2.4
			s.d.	0.27	0.30

All measurements were made with a torque of 0.35 N m

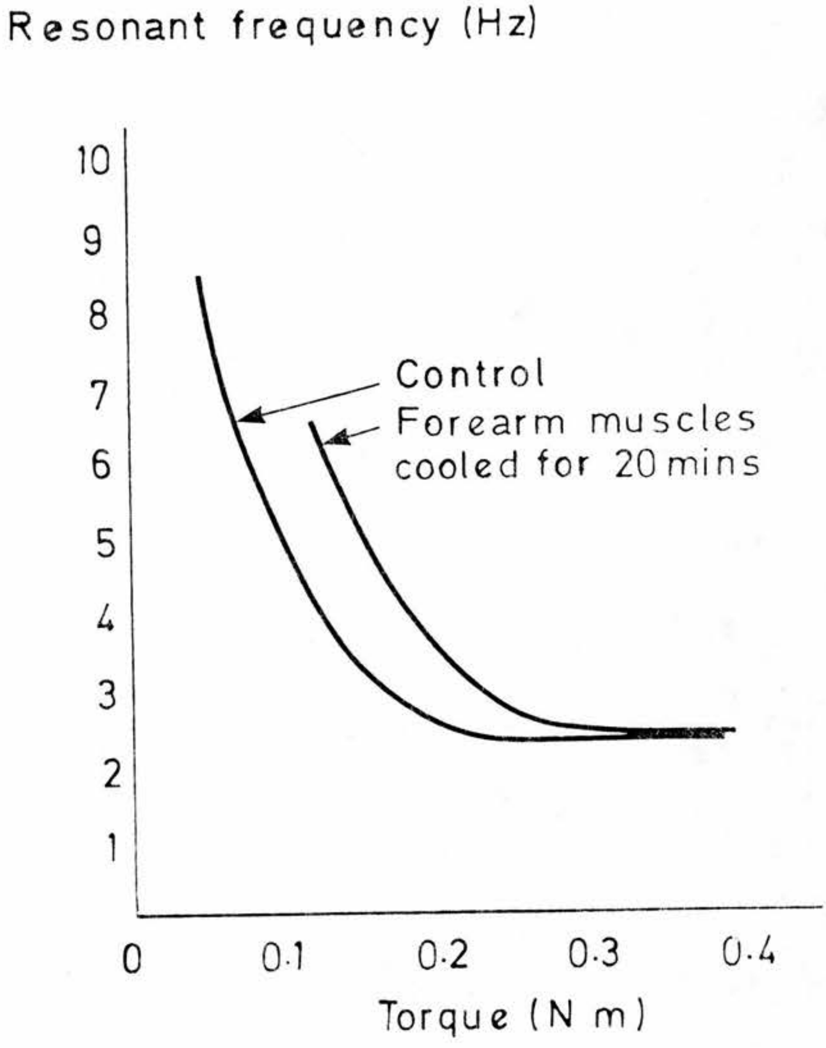


Fig. 3.35 Torque vs resonant frequency after cooling of the muscles. The effect of muscular cooling is to raise the torque threshold; that is, the stiffness of muscle for small forces is increased. The resonant frequency at higher torques is not significantly altered; in this subject it is slightly raised. After cooling the wrist was no longer resonant at torques smaller than 0.15 N m; the damping had increased.
(Subject K.F. 20 m right wrist).

change in the resonant frequency for high values of torque, but there is a change in the pattern of non-linearity; the cooled wrist becomes non-linear at a higher value of torque. The effect of cooling is to increase the torque threshold; the wrist is now stiffer for small forces than it was previously. This increase in stiffness is not associated with an increased EMG; on the contrary, the EMG, recorded either with surface electrodes or with fine wires in the muscle, is silent.

3.4)2 Cooling and compliance.

The effect of cooling the forearm muscles was investigated in 17 subjects. In 10 of these subjects (Group A) cooling was produced by simple immersion of the arm in cold water, the remaining seven (Group B) were cooled using the water filled arm bath described in the resonant frequency experiments.

The effect of cooling on wrist compliance, measured with rectangular torques, was dramatic. In all group A subjects cooling of the forearm muscles decreased compliance of the wrist by more than 50%. Five subjects cooled only the hand and wrist by immersion in water; this procedure did not affect compliance in four subjects, but in the fifth there was a decrease of approximately 20%. The influence of cooling on compliance, water temperature, and immersion time, for the 10 subjects is summarised in table (3.12). In these measurements the compliance has been calculated as the displacement produced by a 0.5 N m torque delivered as a slowly reciprocating rectangular wave (0.5 Hz). The difference in compliance produced by cooling was highly significant.

Table 3.12 The influence of forearm coding on wrist compliance.

Subject	Age (yr)	Sex	Wrist	Water temp. ^{o}C	Cooling time (mins.)		Control Compliance rad N m^{-1}	Cooled Compliance rad N m^{-1}
A.O.	20	F	R	10	15		2.86	1.01
J.C.	19	F	R	8	10		2.34	0.93
B.E.	19	F	L	6	10		1.95	0.76
S.C.	19	F	L	6	20		2.52	1.25
J.S.	20	F	L	7	15		1.47	0.50
K.F.	19	F	L	6	15		2.35	0.91
M.P.	19	M	R	8	15		1.38	0.30
S.G.	19	M	R	8	10		2.01	0.28
I.G.	22	M	L	10	15		1.97	0.57
K.F.	20	M	R	9	15		2.13	0.56
						Mean	2.09	0.71
						s.d.	0.43	0.32

All measurements were made with a rectangular torque (0.5 N m) at 0.5 Hz.

Detailed information about what happens to the stiff region in cooling was obtained by plotting composite compliance curves for the 10 group A subjects before and after cooling. The results from all the subjects tested showed a similar pattern; fig (3.36) is typical. Cooling decreases considerably the overall compliance, thus in fig (3.36) the compliance for torques of 0.4 N m is decreased from 1.4 rad N m^{-1} to 0.6 rad N m^{-1}. The size of the stiff region is also increased.

Cooling with water at less than 8°C was to some extent a "heroic" procedure; discomfort was experienced at first as the skin became cold. When the experiment was repeated with water at 10-12°C only very slight discomfort was experienced and the compliance was still greatly reduced. In fact, considerable reduction in compliance has been observed with water temperatures as "high" as 17°C. As the temperature of the muscles could not be directly determined, no attempt was made to correlate between degree of cooling and stiffness.

The converse experiment was attempted, and water at a temperature of 46°C was circulated around the arm. No change in compliance was noted. There are two possible interpretations of this. Firstly, it is possible that warming the arm in this way is ineffectual as the rest of the body acts as a heat exchanger and the circulation continuously carries away heat from the warmed limb. The second possibility is that warming muscle does not increase its compliance.

Using the forearm bath, it was possible to monitor the development of these changes (group B). When water at 4-5°C was passed through the bath, a decrease in compliance was noted

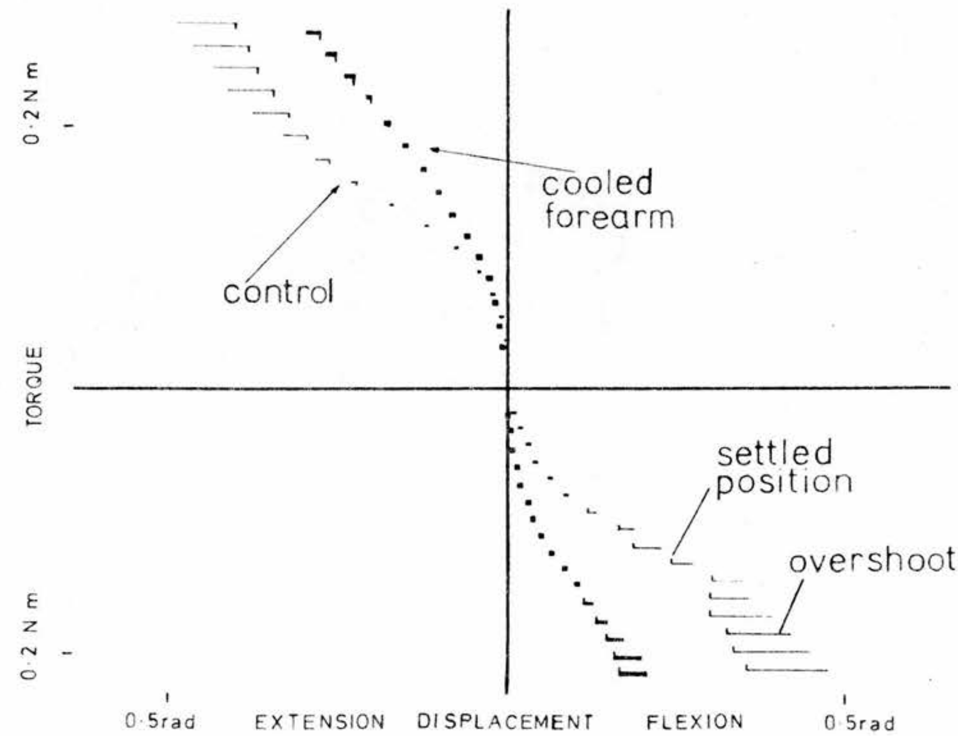


Fig. 3.36 Composite compliance curves before and after cooling of the muscles. Cooling decreases the overall compliance to about 50% of its control value. The size of the stiff region is increased.
(Subject L.R. 22 f right wrist).

after a delay of five to 10 minutes. This decrease reached a maximum after a further 10 minutes or so. Cooling was prolonged for more than 80 minutes in two experiments and no further decrease in compliance was noted, nor was there any tendency for the compliance to increase spontaneously. Skin temperature was recorded using a multi-channel telethermometer, but there did not appear to be a useful correlation between skin temperature and compliance. The skin temperature fell soon after the cold water was circulated through the bath, and stayed low for the duration of the experiment. The onset of decreasing compliance coincided with subjective impressions of increasing muscle stiffness.

In four experiments EMG was monitored by fine silver wires implanted in flexor and extensor muscles. Myotatic activity was not observed, and the decreased compliance could not be related to increases in tonic EMG activity. After cooling for 10 minutes or more, voluntary movements became slow and laborious; at normal temperature most subjects can perform alternating movements of the wrist at frequencies in excess of 8 Hz; when cooled, movements at 2 Hz became difficult.

3.4) 3 Thixotropy

Cooling of the muscles has profound effects on thixotropy but these effects are difficult to quantify using low amplitude sinusoidal analysis. Cooling of the muscles increases the stiffness of muscles for small sinusoidal forces (this is shown by the elevation of the torque threshold in the resonant frequency experiments). Accordingly, in the cooled state a larger driving force is required in order to obtain the same amplitude as when the muscles are at normal temperature.

Stirring the system leads to a large increase in amplitude, larger than that observed at normal temperatures, but it is impossible to say whether this should be attributed to the cooled muscles, or whether it is because the driving force is larger than was necessary at normal temperature.

The time required for the muscles to revert to their low compliance is increased by cooling; the force must be cut for three or four times as long to permit the system to regain its original low compliance. Thus the effect of cooling is to exaggerate the thixotropic changes, and make them more obvious; it is an everyday observation that when we become cold our muscles become stiff, and active or passive movements are very effective in overcoming this stiffness.

During the cooling and compliance experiments it was possible to provide a dramatic demonstration of the dependence of muscle compliance on the past history of movement. In fig (3.37) a ramped rectangular wave is applied to the wrist of a male subject. The forearm muscles had been cooled for 20 minutes at $7^{\circ}C$, and the overall compliance had decreased considerably. At 'A' the subject made several voluntary flexion/extension movements and for the following cycle of ramped torques the overall compliance is considerably increased, almost reaching the control value. When the cycle of movement ceases and the wrist comes to rest, the muscles revert to their low compliance - this is shown by the next ramped torque cycle. This relatively long term change in compliance is not seen at normal temperature. Small passive movements are also effective in increasing the compliance.

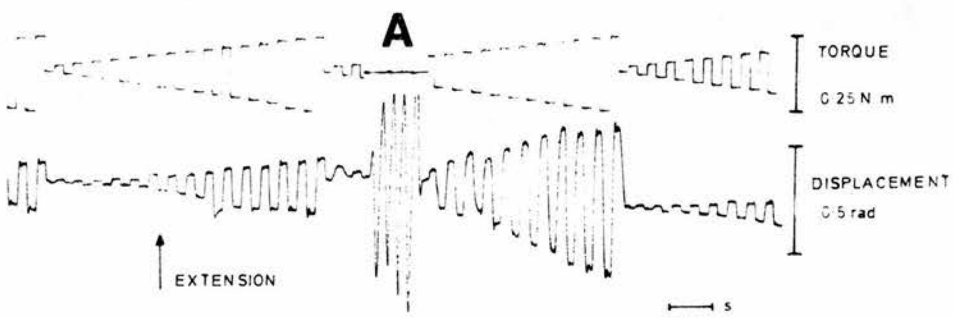


Fig. 3.37 "Thixotropy" in cooled muscle. This record was obtained from a wrist following immersion of the forearm in water at 7°C for 20 mins. Originally the compliance is low (about 30% of the control value). At "A" the subject made 4 flexion/extension movements of the wrist and as a result the compliance during the next cycle of ramped rectangular torques was increased considerably.

At the end of the cycle, when the torque again becomes small, the compliance decreases to its former low level. This type of "long lasting" thixotropic behaviour is not seen in muscles at normal temperature.
(Subject J.T. 22 f right wrist).

This provides an explanation for the paradoxical results of the resonant frequency experiments and the compliance measuring experiments with cooled muscles. The stiffness of the muscles is not increased significantly when assessed by the resonant frequency method because the driving wave form maintains the system in motion and stiffness does not develop. Only with the smallest torques, which presumably are inadequate to prevent stiffness occurring, does the resonant frequency increase. When rectangular torques are employed, the wrist spends much of the time at rest and is therefore stiff. Active or passive movements of the cooled muscles will temporarily reduce this stiffness, but only if the applied rectangular torque is large enough to keep the system in motion.

4) DISCUSSION AND CONCLUSIONS

4.1) Discussion

4.2) Conclusions

4.1 DISCUSSION

4.1) 1 Introduction.

Muscle tone has been assessed in a number of subjects using a printed armature electric motor to apply torques to the joint under test. Quantitative investigations were confined mainly to the wrist, but other joints were investigated, and appear to act generally in the same way.

Rectangular and sinusoidal torques were employed, and the results of these investigations are complimentary. In addition, a low amplitude sinusoidal waveform was used to provide a dramatic demonstration of the non-linear properties of the postural system. The effect of cooling was also investigated, and this was found to increase the stiffness of the muscles.

Experiments involving recording of EMG activity and the use of neuromuscular blocking drugs made it possible to determine the contribution to normal relaxed muscle tone made by the nervous system.

Simple techniques have been described which can measure the stiffness of a joint, giving a numerical value for muscle tone. Alternatively, the compliance of the joint can be plotted directly, and the difference between static and dynamic stiffness clearly demonstrated.

It is now intended to draw together the results of the experiments, and summarise what has been learned about muscle tone, and its measurement. A simple theory to account for the profoundly non-linear properties of the postural system, at normal and lowered temperatures, is advanced.

4.1)2 Non-linear stiffness.

The stiffness of the limbs is non-linear; they are disproportionately stiff for small forces. This is shown clearly by the ramped rectangular (page 188) and composite compliance (page 190) experiments, and the elevation of resonant frequency when small driving forces are employed (pages 133 and 139).

Resonant frequency analysis reveals that the stiffness of the wrist is very nearly linear for sinusoidally varying peak torques that are greater than a certain threshold value; this threshold value is significantly greater in men than in women, although there is some overlap between groups (pages 136 and 138). However, if the peak amplitude and peak velocity at resonance are studied (pages 146 and 148), it is apparent that the transition from a stiff non-linear system to a less stiff approximately linear one occurs at nearly the same peak amplitude (and velocity) in men and women. It therefore appears possible that the behaviour of the wrist may be related not to the size of the applied force but rather to the resulting amplitude, or velocity, attained.

What could cause this amplitude, or velocity, related stiffness? The bulk of the evidence suggests that it is a reflection of the well documented stiffness of skeletal muscle for small displacements. There are, however, two other possibilities which can be examined first.

1) The stiffness for small displacements might be caused by the anatomical arrangement of the joint. Stone, Thomas and Zakian (1965) demonstrated that the eyeball of the dog is very stiff for small movements, both in response to statically applied stretch and sinusoidally varying torques. They suggested this

was due to "pretensioning" of the extra-ocular muscles. In the resting position the eye was subjected to the extra tension of these opposed muscles and was therefore less easily displaced. It appeared possible that an analogous mechanism might be operative at the wrist, and the stiffness for small displacements might be due to pretensioning of the forearm muscles.

However, when the wrist was biased from its resting position by superimposed torques, the pattern of non-linearity and the size of the "stiff region", was not altered (pages 155 and 192). Thus, pretensioning cannot be responsible for the non-linearity of the wrist, and the latter cannot therefore be an anatomical feature of the joint geometry. (Stone _et_ _al_. did not investigate the effect of biasing the eyeball from its resting position).

2) The stiffness of the wrist for small displacements may be a reflection of non-linear properties of synovial fluid in the joint or tendon sheaths.

There are several experimental observations that do not support this assumption. First, cooling the muscles of the forearm has been shown to decrease considerably the compliance of the wrist (pages 204 and 202) and to change the pattern of non-linearity (page 200). During these experiments the joint itself was not deliberately cooled. Conversely, when the hand and joint alone were intentionally cooled, there was no change in resonant frequency or compliance (page 198).

Secondly, the stiff region is present in all the joints investigated, which differ considerably in their anatomical arrangement.

It therefore seems most likely that the non-linear stiffness of the joints is an inherent property of the muscles with which they are associated. Supportive evidence for this also comes from the sex difference in torque thresholds. The torque threshold is greater in men than in women and other investigations (mentioned in section 3.2)8, page 166) point to men having about 90% greater muscle mass. The greater torque threshold for male subjects is therefore a reflection of the extra torque that is required to attain the critical displacement or velocity threshold, because the inherently greater damping of bulky male muscles decreases the amplitude and velocity at resonance by about 50% for a given torque.

The stiffness of skeletal muscle for small displacements has been well documented in in vivo and in vitro experiments in animals. This phenomenon has been attributed to the passive properties of relaxed muscle; it is not neurally mediated. This has been clearly shown to apply also in human muscle; anaesthesia and neuromuscular blockade did not interfere in any way with the stiff region (page 143), which was not associated with recordable EMG activity.

The experiments that other investigators have performed on in vivo or in vitro preparations have invariably employed some form of linear puller; this has the advantage that the amount of stretch or tension in the muscle under test can be measured with precision. In experiments of the type undertaken here it is difficult to relate rotation of the wrist to a linear length change in the stretched muscles. However, if an estimation of this is made it is possible to compare the value obtained with the results of the animal experiments.

4.1)3 Size of the stiff region.

The resonant frequency experiments have shown that the total size of the stiff region is 0.31 - 0.36 rad (page 146). Rectangular torques reveal a smaller range, less than 0.2 rad (pages 188 and 190). Thixotropic changes in compliance have only been seen clearly when the initial displacement is less than 0.1 rad (page 173). If the size of the stiff region is estimated at 0.25 rad, and the effective radius of action of the muscles 1.5 cm (section 3.2)8), this represents a length change of approximately 0.4 cm. However, some of the muscles of the forearm have a fusiform arrangement, and others are pennate, so it is less misleading to express 0.25 rad as a percentage of the total range of movement, which is about 2.5 rad for most subjects. The stiff region therefore extends for about 10% of the total range of movement.

How does this compare with the results obtained by other workers using isolated animal muscles?

D.K. Hill (1968), using the sartorius muscle of the frog and toad, described a special kind of elasticity for small displacements which he named the short range elastic component (SREC). This was seen only for very small length changes, up to more than 0.2% of the muscle length. This elastic property: "provides a simple, almost 'spring-like' resistance at the start of a change of length made even at a very low velocity".

If the length change continues at a constant velocity after the "elastic limit" is reached, the tension which has been developed in the SREC is maintained at a constant level, and this provides a "sort of frictional resistance to further elongation".

Rack and Westbury (1974) described a "short range stiffness" (S.R.S.) in the tetanized soleus and lateral gastrocnemius muscles of the cat. The muscles resisted a small movement, or the first part of a larger movement, with a short range stiffness that did not further increase as the movement continued. The S.R.S. was essentially elastic; little work had to be performed in driving the muscle through a cycle of movement, if this was small. With larger amplitudes the system was dissipative, and this was largely velocity dependent. The S.R.S. persisted for up to about 0.8 mm of stretch (3% length change) although the exact limit was not determined.

Nichols and Houk (1976), using the soleus muscle of a cat, unstimulated, and stimulated at physiological rates, demonstrated a similar stiffness for small displacements. This extended for $\pm$ 60 μm or 0.2% of the length of the muscle, which is the same length change as that reported by Hill (1968).

Denny-Brown (1929) described a "preliminary" or "stationary" rigidity which was present in the flexor and extensor muscles of the cat. He did not state the range over which this rigidity operates, but suggests (in fig. 1) that in the cat semitendinosus it extends for at least 1 mm of lengthening. The length of a cat semitendinosus muscle is about 50 mm so this is a 2% length change.

There is therefore no general agreement amongst this group of workers; Hill and Nichols and Houk maintain that the stiffness for small movements extends for only about 0.20% of the muscle length, whereas Rack and Westbury show that it persists for at least 3% of the muscle length in active muscle. In passive muscle, Denny-Brown's stationary rigidity apparently extends over about 2% of the muscle length.

The S.R.E.C. and S.R.S. are really synonymous with the stationary rigidity of Denny-Brown and as this term has the sanction of longer usage it will be employed in this discussion.

Part of the reason for the lack of agreement is that these workers have expressed the size of the stiff region in different ways. Units of length, percentage length of the muscle and percentage of the physiological range of the muscle have all been employed. These latter two are not the same. As stated earlier, the stationary rigidity in man apparently extends over about 10% of the physiological range of the forearm muscles. Assuming that the physiological range of these muscles is about one third of their length (Cooper and Glassow, 1972) this indicates that the stationary rigidity extends over about 3% of the muscle length. Because of the pennate arrangement of some of the muscles, and the compliance of the tendons, this may be a considerable over-estimation. The magnitude of stationary rigidity in man therefore seems to be comparable with at least some of the animal work.

A simplistic theory, based on the above animal work and the present experiments in man, would be that externally applied forces to the wrist joint will be met with a large resistance, unless their size is sufficient to stretch the muscles of the forearm by more than about 3% of their resting length. The system can therefore have two values of stiffness, a "static stiffness" for small amplitudes, or a smaller "dynamic stiffness" for larger movements.

However, the experiments performed have shown that the presence of a "stiff region" may not only be related to a critical amplitude of movement in the postural system of man; other more complex factors are undoubtedly involved. Two important additions must therefore be made to this simple theory.

1) The stationary rigidity has been shown to be dependent on the prior history of movement of the muscles.

Denny-Brown (1929) was clearly aware of the dependence of stationary rigidity on the prior movement of the muscle under investigation, although there are ambiguities when he describes the time for which the effect persists. In the text the time is described as very short, "less than 1/10 second", but in fig. (1) stationary rigidity is decreased by approximately 50% 3 seconds after a stretch.

The only other investigators who appear to have noted the history dependent stiffness of muscle are Buchthal and Kaiser (1951), and to these investigators belongs the credit for first employing the word "thixotropy"* to describe it. These investigators showed that the overall resistance to stretch of a frog muscle was decreased by the stretches to which it had previously been subjected, and that this decrease persisted for "several minutes". It is perhaps significant that these experiments were performed at low temperature, and in man low temperature enhances the thixotropic effect (page 207).

Hill's hypothesis is that the S.R.E.C. is caused by bonds between the thick and thin filaments of striated muscle; these bonds act as springs and provide a high degree of tension for

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* Although we may now associate the word thixotropy with paint or glue, it is in fact a biological term coined by Peterfi (1927) who used it to describe the sol-gel-sol transformation which he observed in the protoplasm of sea-urchin larvae during movement.

movements that are not large enough to rupture them. For movements that are greater than this critical range they become dissociated, and compliance increases. Buchthal and Kaiser were of course working before the sliding filament theory of muscular contraction, and they were therefore unable to account for thixotropy of muscle in these terms. However, it seems a tenable hypothesis that the bonds between thick and thin filaments require some time to reform completely following rupture. Thus, stationary rigidity will not be apparent until muscle has been at rest for some time. With movements above a certain threshold velocity the bonds will be unable to reform, but for slower movements they will reform continuously, as fast as they are ruptured.

Clear evidence that the compliance of the postural system depends on its prior movements has been presented. With a small sinusoidal torque the resulting amplitude can have two very different values, depending on whether the system has been "stirred" (page 170). It is surmised that stirring dissociates the bonds between thick and thin muscle filaments and the resulting increase in compliance permits a higher displacement and velocity to be attained. While this increased movement persists the bonds are not permitted to reform, and the increase in compliance is self-perpetuating. If the system is allowed to come to rest for more than a short time, the bonds reform, and compliance decreases. Similarly, with slightly larger driving forces the response "grows" spontaneously as the bonds progressively rupture (page 173). Thus, stationary rigidity is appropriately named, for it disappears with appreciable movements.

The largest percentage increase in displacement following stirring occurs at a frequency which is near the resonant frequency in the linear range (page 174). The reason for this is that the increased compliance following stirring results in lowered resonant frequency, which more nearly corresponds to the frequency of the driving waveform. It is, however, evident at higher and lower frequencies. The analogy with a thixotropic substance is therefore very appropriate; with small movements the system resembles a gel, being stiff and springy. With larger movements a gel - sol transformation occurs and the stiffness decreases. The memory time, which is the time necessary for the reverse sol - gel transformation to occur, has not been precisely determined, but appears to be less than 2 s at normal temperatures.

Stationary rigidity is in a sense a nebulous phenomenon which is only present when the muscles are at rest, and have been at rest for some time. The expression that is sometimes used to describe such thixotropic behaviour is "false body" and this seems very appropriate in the present context.

2) It is possible that the transition from static to dynamic stiffness is related to the velocity of the system, rather than its displacement. Certainly the experiments in which the wrist has been biased from its natural equilibrium position have shown that the absolute length of the muscles is unimportant, and the animal experiments cited have shown that stationary rigidity is a property of resting muscle regardless of its resting length. In general, however, the animal experiments cited have not investigated the relationship between stationary rigidity and velocity of stretching.

The resonant frequency experiments have shown (page 148) that the stiffness of the wrist may be related to velocity of movement, with the transition from dynamic to static stiffness occurring at about 2 rad s^{-1}. However, on the basis of the present evidence, using applied torques, where the resulting displacement and velocity are mutually dependent, it is impossible to state unequivocally whether displacement or velocity is the critical factor. It is quite possible that displacement, velocity, and other higher derivatives may all be important.

Because of the thixotropy of the system it is impossible to identify a single critical factor. This is shown clearly in fig. (3.26) (page 180) where ramped positive velocity feedback was applied to the wrist. The torque, displacement, and velocity at which static stiffness develops are all clearly different for increasing and decreasing torques. The threshold is profoundly altered by prior stirring of the system. With this, evidently complex, system it is at present only possible to use the rather vague term "movement" and to state that the compliance of the postural system can be greatly decreased by prior movements to which it is subjected.

It is perhaps best to consider muscle tone as made up of two components: a static rigidity which is seen for small movements, and a smaller dynamic stiffness which is seen with larger movements. The transition from dynamic stiffness to static stiffness is not instantaneous, but requires movement to cease for some time. Such a mechanism fulfills admirably the conflicting requirements of the postural system. It can help to maintain a desired position without the expenditure of energy, and, after a brief period of limbering up, execute rapid movements with little internal resistance.

4.1) 4 Damping.

Peak amplitude and peak velocity at resonance are both indicators of the damping of the limb. Damping is brought about by frictional and viscous resistance of the muscles, and also presumably to a lesser extent by the joint and its associated ligaments.

There is a very obvious sex difference; the velocity and amplitude at resonance attained by the female subjects is on average about double that of the male subjects for the same torque (pages 146 and 148). As in the difference in pattern of non-linearity, this sex difference in damping is evidently a reflection of the larger bulk of muscles in the male subjects. Most authors are agreed that women have on average about 55-60% of the muscle bulk of men, and this fits the observed difference in damping satisfactorily.

The damping of the wrist is effectively linear for torques. greater than about 0.06 N m; this is shown clearly in figs (3.15) and (3.16), where the amplitude and velocity at resonance both increase proportionally with torque. With smaller torques, there is some evidence that the damping of the wrist is non-linear, the amplitude and velocity are disproportionately small and the "Q" is also apparently decreased at the lowest torque levels (page 139). When ramped rectangular torques are employed, the initial 4 or 5 torque pulses do not produce an overshoot, and after this overshoot and rebound develop rapidly (page 188).

This non-linear damping is probably a reflection of static friction in the motor. Evidence that it may be artefactual comes from repeating some of the observations with the modified G6M4 motor; the same elevated resonant frequency is observed at low torque levels, but the sharpness of tuning is much greater. If this is a non-linearity introduced by the driving system, it is only significant at the lowest levels of torque. These levels are lower than the "torque threshold" for increased stiffness; non-linear stiffness cannot therefore be caused by the same artefact.

4.1)5 EMG.

The most striking feature of EMG recording was the absence of stretch reflex activity. Even when large rectangular torques were employed, phasic stretch reflexes were not observed, except in some poorly relaxed subjects, or occasionally in other subjects when they were disturbed or distracted. Tonic stretch reflexes were never seen in normal relaxed subjects (section 3.1)2).

However, the opposite pattern of electrical activity, the shortening reaction, was often seen both with rectangular and sinusoidal torques. The significance of this activity is uncertain; the role of the shortening reaction may be to contract a muscle when it is passively shortened, and thus "take up the slack". In most subjects the shortening reaction tended to come and go, and its presence did not alter the resonant frequency or compliance.

When EMG activity was generated by voluntary co-contraction the stiffness of the wrist was considerably increased, both as assessed by resonant frequency (page 116) and compliance (page 185). The exact relationship between EMG activity and stiffness could not be determined; theoretically a fourfold increase in EMG might be expected to double the resonant frequency. The actual relationship is shown in fig. (3.8) (page 130); more detailed analysis has not been attempted, because of the difficulties in ensuring that the EMG recorded is a representative sample of the total activity, and because the EMG must be integrated over a period of time in which the stiffness and instantaneous frequency may vary.

With spastic subjects tonic and phasic EMG activity was recorded from the affected limb, and the resonant frequency was more than doubled (page 118). The compliance of these subjects was therefore much less than normal.

Cooling has been shown to bring about a substantial increase in the static stiffness of the muscles (pages 200 and 204). This increased stiffness is not accompanied by EMG activity; it is a consequence of changes in the passive mechanical properties of resting muscle. Cooling is frequently claimed to bring about an increase in muscle tone which eventually culminates in generalised shivering. The metabolic consequences of the increased tone are generally supposed to restore the temperature of the body. For example, Schmidt (Fundamentals of Neurophysiology, 1978):

> "thus by varying the muscle tone the body can greatly vary the amount of heat it produces, and this capability can be put to use in regulating body temperature at various ambient temperatures".

It seems very unlikely that the purely passive increase in muscle tone which has been shown to follow localised cooling can have metabolic consequences of this type, but it is possible that generalised whole body cooling has different effects. Interestingly, it has recently been suggested that non-shivering thermogenesis may occur in brown adipose tissue, rather than in muscle (for example, Rothwell & Stock, 1979).

4.1)6 Measurement of muscle tone.

Resonant frequency

For small sinusoidal torques the response of the postural system to stretch has been shown to be highly non-linear, but above a certain torque threshold the response becomes virtually linear. Since, above the torque threshold, the resonant frequency is linear the dynamic stiffness evidently has a constant value. Below this threshold value the stiffness progressively increases as the torque is further reduced; the static stiffness is therefore non-linear, being greater for the smallest torque. This bi-phasic behaviour has been clearly illustrated using swept sine waves (pages 133 and 136) and ramped positive velocity feedback (page 180). Any attempt to assess muscle tone using sinusoidal torques therefore yields a result that depends on the size of the torque employed.

With torques that are larger than the threshold value a constant value of stiffness will be obtained; this is the dynamic stiffness of the postural system. With torques that are less than the threshold value a higher resonant frequency will be obtained because of the greater size of the static stiffness. The size of this stiffness depends on the torque employed to measure it. The resonant frequency method is therefore best suited to obtaining information about the dynamic component of muscle tone.

An appropriate torque (0.3 N m at the wrist) must be employed so that the system operates in its linear region. This torque is greater than the torque threshold for men and women, but it is not so large that it causes excessive peak displacements of the wrist, and reaches the anatomical limits of the joint, causing involuntary stiffening (page 134).

Measurements of this type were performed on a number of subjects and the results were calculated by adding inertia to the system. This approach also permitted the inertia of the hand to be determined. The results of this analysis (pages 164 and 165) confirm that the male subjects had, as a group, larger values of stiffness and inertia. This is presumably due to the extra bulk of muscle of the male subjects. There was no apparent systematic difference between left and right wrists, and statistical analysis was not worthwhile with the relatively small number of subjects tested.

The dynamic stiffness of the wrist ranged between approximately 0.5 and 1.5 N m rad^{-1} in the subjects tested; it is anticipated that if a larger number of male and female subjects were to be tested, two normal distribution curves would be obtained, and there would be a generally higher value of dynamic stiffness amongst the male population. This difference would be a reflection of the larger amount of muscle in men.

Rectangular torques

Rectangular torques were employed in an attempt to provide a direct method for the determination of compliance.

In principle, the compliance of a system can be assessed by applying a slowly increasing force, which will result (theoretically) in a slowly increasing displacement. This static form of analysis cannot be employed to test the postural system, or any other system that has a static stiffness which is effectively greater than the dynamic. Under such conditions, when the "elastic limit" of the static stiffness is reached the displacement will suddenly increase in an uncontrolled way. Static methods of this type therefore cannot be used in the analysis of muscle tone.

One way of overcoming this difficulty is to use rectangular torques so that the displacement for a single pulse of applied torque can be determined (pages 183 and 185). The use of a rectangular torque in this way presupposes that the resulting displacement can be measured from a fixed baseline. However, the experiments in which ramped monophasic torques were employed have demonstrated that this baseline is indefinable, and is dependent on the forces that have previously been applied to the joint. Thus, when a pseudo-random train of different sized torque pulses was applied to the wrist, the size of the response was determined as much by the size and direction of the previous pulses as by that under investigation.

Another problem is that subjects may react to slowly repeating waveforms, and this obviously gives unpredictable results. Muscle tone cannot therefore be assessed satisfactorily by applying single pulses of torque to the postural system and analysing the displacement.

However, if a rapidly repeating train of ramped rectangular torques is employed (composite compliance method) satisfactory results can be obtained. The torque reverses rapidly so that the system is at rest only for a short time, and since a pattern of torques is applied, any anomalous response is immediately obvious and can be disregarded. This method has the advantage that the non-linearity of the postural system is immediately visible and the tone of the muscles is recorded graphically. It might appropriately be termed a "pseudo-static" technique.

When a ramped series of torques is employed in this way the results are to some extent artificial, as each displacement recorded is dependent on the previous movement. The baseline is, as it were, continuously created. The advantage of this is apparent in fig. (3.33) (page 194) where the resting position of the wrist could otherwise have drifted by as much as 0.3 rad. An inevitable consequence is that a slightly different pattern is therefore obtained when the torque pulses are made to decrease rather than to increase, or when the repetition rate is altered.

Composite compliance curves have provided a useful method for investigating the response of the postural system to applied forces, and the results are at least qualitatively similar to those obtained by sinusoidal analysis. The system is evidently disproportionately stiff for the smallest torques. The size of the stiff region assessed in this way is approximately the same as when sinusoidal torques are employed. (figs. 3.11, page 138, and 3.31, page 191). With larger torques the system becomes very much more compliant, although the slope of the curve (fig. 3.31) shows that it is not entirely linear in this region as it was when sinusoidal torques were employed. This is probably because with ramped rectangular torques the system spends an appreciable time at rest, whereas with sinusoidal torques it comes to rest only at the turning points of the movement.

By employing a ramped series of torque pulses in quick succession, the transition from static to dynamic stiffness is demonstrated. Ramped rectangular torques therefore provide valuable information about the static and dynamic components of muscle tone.

Either rectangular torques or sinusoidal torques can therefore be employed to obtain information about muscle tone. When sinusoidal forces are used, it is important to be sure that the system is operating in its linear region, and when rectangular torques are used it is important to use a ramped series of torques in order that each torque pulse can "condition" the system for the next, and the pattern of non-linearity can be observed.

With sinusoidal torques, resonance can be obtained either by sweeping the frequency over an appropriate range or by the use of positive velocity feedback which automatically drives the system at its resonant frequency. If swept sinusoidal torques are employed, the rate of sweeping must not be too rapid; this allows the motion that is due to transients to die away (page 122).

This insight into the nature of muscle tone explains why previous attempts to measure it have often met with little success. Methods that are static, and rely on the application of slowly changing torques to the system, are doomed to failure because of the dependence of the stiffness of the musculature on movement. Clearly, a system of this type, which has been shown to be sensitive to the amplitude or velocity of stretch, or both, cannot have its stiffness measured in this way. Dynamic methods, where the force is delivered instantaneously as a rectangular pulse, are better, as each pulse produces a definable displacement. The problem here is that the baseline from which these measurements are made has itself been shown to depend on the previously applied forces. Similarly, the actual compliance of the muscles depends on previously applied forces.

Furthermore, the compliance of the postural system is extremely non-linear; information about the response of the postural system to one particular size of torque is not very useful, as this information cannot be extrapolated for bigger or smaller torques. A ramped series of torques has not been employed in previous investigations. Resonant frequency analysis of muscle tone, which yields reliable and consistent results, has not been extensively employed, and these few previous investigations have not used addition or subtraction of inertia or stiffness so that numerical values for muscle tone can be obtained.

4.1)7 Cooling of the muscles.

Cooling of the muscles has profound effects on muscle tone. Cooling the forearm muscles has no effect on the resonant frequency of the wrist when high torque levels are employed. Evidently the dynamic stiffness of the muscles is not affected by this procedure (page 199). However, the pattern of non-linearity is altered and the resonant frequency starts to rise at a greater torque than at normal temperatures (page 200). Therefore, as assessed by resonant frequency analysis, the size of the stiff region (static stiffness) is increased, although the dynamic stiffness is not.

It seemed possible that these changes were due not to cooling of the muscles but rather to cooling of the joint itself; but this was ruled out by experiments in which cooling of the hand and wrist joint only was shown to be without effect. The changes produced are therefore consequent on a reduction in muscle temperature. No direct evidence of a reduction in the temperature of the muscles was obtained, but immersion of the forearm in still water at temperatures of 12 - 30°C has been shown to result in a corresponding reduction in deep muscle temperature which is effectively complete after 30 minutes (Barcroft and Edholm, 1943). These investigators showed that, with water temperatures of 12 $^{\circ}$C a temperature of 26°C is reached by the brachioradialis muscle at a position which is not far from the centre of the forearm. After 60 minutes the temperature reaches a plateau at about 18°C . The initial temperature of this muscle was 32°C.

It can be safely concluded that well stirred water at the temperature employed in the experiments described, (7-8°C), will have reduced considerably the temperature of all the forearm muscles.

On first examination the results obtained with ramped rectangular torques seem different to those obtained by sinusoidal analysis. The overall compliance of the wrist was reduced considerably by cooling, even when large torques were used (page 202). After 20 minutes at 8°C, for example, the displacement for a given torque was only about 50% of the control value.

It appears that cooling of the muscles emphasises the difference between the static and dynamic stiffness of the muscles. When sinusoidal analysis is employed, the muscles are kept in motion and consequently stationary rigidity cannot develop unless the force is so small that the critical movement is not exceeded. When a rectangular waveform is used the system spends an appreciable time at rest and stationary rigidity can develop. Evidently cooling increases the effect of stationary rigidity; a larger force is required to attain the critical displacement or velocity. This provides an explanation for:-

1) The elevation of the torque threshold.
2) The increase in size of the stiff region as assessed by composite compliance curves.

3) The overall decrease in compliance is caused mainly by an increase in the size of the stiff region. Thus, for any applied force, a larger amount of energy is required to overcome the stationary rigidity, and the resulting displacement is much reduced.

4) The stiff region is dependent on the prior history of movement. This is clearly shown by the effect of active or passive movements on the compliance of the wrist as assessed by ramped rectangular torques. These movements are evidently effective in "freeing" the system, and the system, once freed, takes a longer time than normal to "gel". Cooling has had an effect on the thermodynamics of the sol-gel transformation. Thermodynamic theory predicts that a rise in temperature will favour sol rather than gel and vice-versa. Similarly a decrease in temperature will increase the time taken for the bonds forming the gel to reform and thus increase the "memory time" of the system.

It is noteworthy that all the measures which are employed by physiotherapists and others in the treatment of muscle stiffness involve procedures which have an appropriate effect on a thixotropic system. Thus heat*, e.g. I.R. or S.W. diathermy or from exercise, and mechanical stimuli, e.g. stretching, massage, or vibration, have all been employed in the empirical treatment of muscle stiffness. It is also significant

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* The belief that heat reduces the stiffness of the limbs has a long pedigree, for example: "The motion and activity of the body consisteth chiefly in the sinews, which, when the southern wind bloweth, are more relax."

Francis Bacon 1626
Sylva Sylvarum, p. 381

that the degree of muscular cooling does not have to be very great in order to bring about a large increase in stiffness. Temperatures of the muscles in the peripheral parts of the body may easily be reduced by low ambient air temperature, and immersion of the body in even moderately cold water will quickly cause muscular stiffness in even the central parts.

Patients with Raynauds syndrome, where the bloodflow in the peripheral parts of the body is reduced, may have cold hands, and this is often associated with stiffness of the fingers. Similarly, all sensible athletes, dancers, etc. limber up before exercise, and the increase in compliance that results from this may be due in part to a direct reduction in the size of stationary rigidity, and in the longer term, to the effects on the thixotropic mechanism of the resulting rise in muscle temperature. Warming of the forearm did not increase wrist compliance, probably because localised warming of the muscles does not adequately raise the temperature of the muscles (but cf. Barcroft and Edholm, 1943). However, with whole body warming there may be a general decrease in static stiffness, and perhaps "a warm relaxing bath" is an appropriate description!

4.2 CONCLUSIONS

There are three principal conclusions to be made about the results of the experiments.

First, printed armature electric motors have provided a reliable and reproducible method of investigating the properties of the postural system and measuring muscle tone. A great virtue of this type of torque generator is the versatility of the torque patterns that can be produced. Almost any pattern of applied electrical waveform can be faithfully translated into a corresponding torque. Thus the applied torque pattern is limited only by the scope of the waveform generator and the ingenuity of the operator. The printed motor does not appreciably load the limb to which it is coupled and its friction is very small. Its small size, and high power to weight ratio, permit direct coupling to any joint. The ideal torque generator would have zero inertia, zero friction, and be powerful and very small; the printed armature electric motor is as near to this list of requirements as is possible at present.

The second conclusion centres on the postural system and the nature of muscle tone. Muscle tone has been shown to be highly non-linear; the limbs resist an applied torque with a force that is large at first when the limb is stationary or nearly so, and this force falls off to a lower level after an appreciable movement is made. This non-linearity is almost certainly caused by the properties of relaxed skeletal muscle; Hill (1968) has explained an approximately analagous stiffness for small movements in amphibian muscles as a result of bonding between actin and myosin molecules. An additional, and hitherto unappreciated facet of this behaviour, is that, in man, it confers on the postural system the property of thixotropy. That is, the stiffness of the postural system is highly dependent on its prior history of movement. Much of the apparent stiffness when the system is at rest is in a sense illusory as it disappears when the system is in motion. "False body" is a term that has been applied to this sort of behaviour.

The thresholds for appearance and disappearance of false body in the postural system have not been determined with certainty, but are probably related to the amplitude or velocity of movement. Temperature has been shown to influence the size of the false body; this provides a plausible explanation for the effect of "limbering up". This type of thixotropic mechanism with which nature has provided us is ideally suited to the conflicting requirements of the postural system. It can provide a stable platform which resists perturbing forces, either applied externally to the body, or internally as a result of the action of other muscles. By making a large part of this resistance inherent in the resting muscles themselves the task of the controlling nervous system is simplified, and inappropriate time delays in response are circumvented. Such a mechanism will presumably aid postural stability. Conversely, if the system is called upon to generate movements, these movements limber* up the postural system, and increase its compliance, thus allowing rapid powerful movements to be executed with little internal resistance.

In the light of this new knowledge about the thixotropy of the postural system and the "falseness of our bodies" the reasons for the failure of most previous methods to measure muscle tone become apparent. With a system that has a stiffness which is so

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* limber up may be derived from "limb". (O.E.D.)

dependent on movement it is possible to obtain very different values for muscle tone depending on the size and shape of the force that is employed for measurement. None of these values will be wrong, but equally, none of them can be regarded as right.

It is hoped that this investigation has helped to illuminate this previously unrecognised problem and to suggest methods which will enable the complicated dynamics of the postural system to be investigated further.

Finally, muscle tone has been analysed and measured in a number of volunteer subjects. These investigations have demonstrated that there is a large difference in the postural dynamics of men and women. The principle differences are that the wrists of male subjects are much more heavily damped and that the size of the stationary rigidity is larger. Both these observations are satisfactorily explained by the presence of larger muscles in male subjects.

Interestingly, the resonant frequency of the wrist in all the subjects tested lay between approximately 2 and 3 Hz; this implies that there is a relatively precise balance between the inertia and stiffness of the limb, additional inertia being compensated automatically by extra stiffness. In accordance with this, female subjects have been shown to have smaller values of stiffness and inertia; their hands are smaller and they are "limp wristed".

None of the subjects that were tested were athletes; it would be interesting to know if this sex difference is susceptible to modificiation by training. It is not known whether the fairly constant value of resonant frequency from subject to subject is a "useful" feature. Walsh (1979) suggested that information about resonant frequency may be utilised in the execution of voluntary movements. He proposed that, in making everyday movements, we employ a series of linked resonant levers. If these movements are to be smoothly and economically executed the muscles may have to be activated at the correct point to take account of the resonant nature of the limbs. He suggested that the resonant frequency of the joints is continuously adapted to the requirements of the movement. In learning a new skill this matching is imprecise, and movements are clumsy and wasteful of energy. It may be the role of the cerebellum to bring about this continuous adjustment, and thus alter the "tune of the tone".

REFERENCES

ADRIAN, E.D. and BRONK, D.W. (1929). The discharge of impulses in motor nerve fibres. Part II. The frequency of discharge in reflex and voluntary contractions. J. Physiol. 67, 119-151. [45].*

AGARWAL, G.C. and GOTTLIEB, G.L. (1977). Forced oscillations of the ankle joint. Proceedings of the International Occupational Hand-Arm Vibration Conference. Edited: Wasserman, D.E. and Taylor, W. Pub. U.S. Dept. of Health Education Welfare. (Ohio). [41, 172].

AGATE, F.J., DOSHAY, L.J. and CURTIS, F.K. (1956). Quantitative measurement of therapy in paralysis agitans. J. Amer. Med. Assoc. 160, 352-354. [37].

AINSLIE, A.C. (1979). Logarithmic audio sweep generator. Wireless World, September 1979, pp. 42-47. [67].

ALEXANDER, R.M. (1968). Animal Mechanics. Sidgwick & Jackson, London. [79].

ANGEL, R.W. and HOFMAN, W.W. (1963). The H reflex in normal, spastic and rigid subjects. Arch. Neurol. 8, 591-596. [49].

von ANREP, B. (1880). Studien über tonus und elasticität der muskeln. Arch. f.d. ges. Physiol. (Bonn). Vol. XXI, pp. 226-240. [6].

ASHBY, P. and BURKE, D. (1971). Stretch reflexes in the upper limb of spastic man. J. Neurol. Neurosurg. Psychiat. 34, 765-771. [46].

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* Numbers in square brackets refer to page numbers in text.

BACKLUND, L. and TISELIUS, P. (1967). Objective measurement of joint stiffness in rheumatoid arthritis. Acta Rheum. Scand. 13, 275-288. [167].

BARCROFT, H. and EDHOLM, O.G. (1943). The effect of temperature on blood flow and deep temperature in the human forearm. J. Physiol. 102, 5-20. [229].

BARKER, D. (1948). The innervation of the muscle spindle. Quart. J. Microsc. Sci. 89, 143-186. [13].

BARKER, D. (1967). The innervation of the mammalian skeletal muscle. In: Myotatic, Kinesthetic and Vestibular Mechanisms. Ciba Symposium. (Eds.: de Reuck, A.V.S. and Knight, J.). pp. 3-15. Churchill, London. [14].

BARKER, D., IP, M.C. and ADAL, M.N. (1962). A correlation between the receptor population of the cat's soleus muscle and the afferent fibre-diameter spectrum of the nerve supplying it. In: Symposium on Muscle Receptors. (Ed. Barker, D.). pp. 257-261. Hong Kong University Press, Hong Kong. [15].

BASMAJIAN, J.V. (1967). Muscles Alive: Their Functions Revealed by Electromyography. The Williams and Wilkins Company, Baltimore. [22, 46].

BASMAJIAN, J.V. and STECKO, G.A. (1962). A new bipolar indwelling electrode for electromyography. J.Appl. Physiol. 17, 849. [70].

BASTHOLM, E. (1950). The History of Muscle Physiology. Munksgaard, Copenhagen. [2].

BENEDICENTI, A. (1896). La tonicite des muscles etudiés chez l'homme. Arch Ital. de Biol. 25, 385-417. [34].

BERNHARD, C.G., BOHM, E. and PETERSEN, I. (1953). Investigations on the organization of the corticospinal system in monkeys. Acta Physiol. Scand. 29, Suppl. 106, 79-105. [22].

BERNSTEIN, N. (1967). The co-ordination and regulation of movements. Pergamon Press, Oxford. [34].

BERTHOZ, A. and METRAL, S. (1970). Behavior of a muscular group subjected to a sinusoidal and trapezoidal variation of force. J. App. Physiol. 29 No. 3, 378-384. [30, 40, 110].

BEVENDRE, M. (1961). The Art of Scientific Investigation. Mercury, London. [50].

BIGLAND, B. and LIPPOLD, O.C. J. (1954). The relation between force, velocity and integrated electrical activity in human muscles. J. Physiol. 123, 214-224. [30, 46].

BOSHES, B., BRUMLICK, J., WACHS, H., MIER, M. and PETROVICK, M.L. (1960). Studies of tone, tremor and speech in normal persons and Parkinsonian patients. Neurol. 10, 805-813. [38].

BOYD, I.A. (1956). The tenuissimus muscle of the cat. J. Physiol. 133, 35P. [13].

BOYD, I.A. (1962). The structure and innervation of the nuclear bag muscle fibre system and the nuclear chain muscle fibre system in mammalian muscle spindles. Phil. Trans. Ser. B. 245, 81-136. [14].

BRAUNE, G.W. and FISCHER, O. (1890). Über den Schwerpunkt des menschlichen Körpers. Abhandl. D. Kön. Sächs. Ges. D. Wissehsch. 26, Math. Phys. Classe 15, 559-589. [34].

BRONDGEEST, P.Q. (1860). De tono musculorum voluntati soliditorum (in Dutch). German summary - Untersuchungen über den tonus wilkurlichen Muskeln. Arch. f Anat. Physiol. u. Wissensch. Med. 27, 703-704. [5, 7].

BRUMLICK, J. and BOSHES, B. (1961). Quantitation of muscle tone in normals and in Parkinsonism. Arch. Neurol. 4, 399-406. [38].

BUCHANAN, F. (1908). The electrical response of the muscle in voluntary contraction in man. J. Physiol. 37, xlvii P. [44].

BUCHTHAL, F. and KAISER, E. (1951). The rheology of the cross-striated muscle fibre with special reference to isotonic conditions. Dan. Biol. Medd. 21, No. 7, 5-307. [52, 74, 77, 217].

BULLER, A.J., ECCLES, J.C. and ECCLES, R.M. (1960). Interactions between motoneurones and muscles in respect of the characteristic speeds of their responses. J. Physiol. 150, 417-439. [18].

BURKE, D., ANDREWS, C.J. and LANCE, J.W. (1972). Tonic vibration reflex in spasticity, Parkinson's Disease and normal subjects. J. Neurol. Neurosurg. Psychiat. 35, 477-486. [48].

BURKE, D., GILLIES, J.D. and LANCE, J.W. (1970). The quadriceps stretch reflex in human spasticity. J. Neurol. Neurosurg. Psychiat. 33, 216-223. [46].

BURKE, D., GILLIES, J.D. and LANCE, J.W. (1971). Hamstrings stretch reflex in human spasticity. J. Neurol. Neurosurg. Psychiat. 34, 231-235. [46].

BURTON, R. (1968). Vibration and Impact. Dover Publications, New York. [80, 88, 112].

CARMICHAEL, E.A. and GREEN, F.H.K. (1928). Parkinsonian rigidity - a clinical and instrumental study of the effect of stramonium, hyoscine and other alkaloids. Q.J. Med. 22, 51-58. [36].

CLEMMESEN, S. (1951). Some studies of muscle tone. Proc. Roy. Soc. Med. 44, 637-646. [46].

COOPER, J.M. and GLASSOW, R.B. (1972). Kinesiology. Pp. 81-82. C.V. Mosby Co., St. Louis. [216].

COOPER, S. (1959). The secondary endings of muscle spindles. J. Physiol. 149, 27-28P. [16].

COOPER, S. and DANIEL, P.M. (1956). Human muscle spindles. J. Physiol. 133, 1P. [13].

CORMACK, R.M. and LAMB, J.F. (1981). A class experiment for teaching statistics to physiology students. J. Physiol. 310, 5P. [166].

CREED, R.S., DENNY-BROWN, D., ECCLES, J.C., LIDDELL, E.G.T. and SHERRINGTON, C.S. (1932). Reflex Activity of the Spinal Cord. The Clarendon Press, Oxford. [17].

DAVIES, D.V. (1966). Synovial fluid as a lubricant. Fed. Proc. 25, 1069-1076. [77].

DAVIS, J.F. (1952). Manual of Surface Electromyography. Laboratory for Psychological Studies, Allan Memorial Institute of Psychiatry, Montreal. [98].

DENNY-BROWN, D. (1929). On the nature of postural reflexes. Proc. Roy. Soc. B. 104, 252-301. [17, 27, 74, 215].

DENNY-BROWN, D. (1962). The midbrain and motor integration. Proc. Roy. Soc. Med. 55, 527-538. [114].

DESMEDT, J.E. and GODAUX, E. (1977). Critical evaluation of the size principle of human motoneurones. Recruitment in ballistic movements and in vibration-induced inhibition or potentiation. Trans. Amer. Neurol. Ass. 102, 104-108. [19].

DESMEDT, J.E. and GODAUX, E. (1978). Ballistic contractions in fast or slow human muscles: discharge patterns of single motor units. J. Physiol. 285, 185-196. [19].

DIETRICHSON, P. (1973). The role of the fusimotor system in spasticity and Parkinsonian rigidity. New Developments in Electromyography and Clinical Neurophysiology 3, 496-507. Ed. Desmedt, J.E. Karger, Basel. [48].

DINTENFASS, L. (1962). Thixotropy of blood and proneness to thrombus formation. Circulation Res. 11, 233-239. [77].

DOSHAY, L.J. (1938). Graphic rigidity index. Preliminary Report. J. Mt. Sinai Hosp. 5, 451-462. [37].

DOSHAY, L.J. (1964). Summary: Thirty years progress in hypertonic quantifications. Cl. Pharm. Therap. 5, 961-966. [37].

DRILLIS, R. and CONTINI, R. (1966). Body segment parameters. Technical report 116.03. New York University School of Engineering and Science. [109].

DUGGAN, T.C. and MCLELLAN, D.L. (1973). Measurement of muscle tone: a method suitable for clinical use. Electroenceph. Clin. Neurophysiol. 35, 654-658. [42, 111].

ECCLES, J.C., FATT, P. and LANDGREN, S. (1956). Control pathways for direct inhibitory action of impulses in largest afferent nerve fibres to muscles. J. Neurophysiol. 19, 75-98. [21].

ECCLES, J.C. and SHERRINGTON, C.S. (1930). Numbers and contraction-values of individual motor-units examined in some muscles of the limb. Proc. Roy. Soc. B. 106, 326-357. [11, 18].

ELDRED, E., GRANIT, R. and MERTON, P.A. (1953). Supraspinal control of the muscle spindles and its significance. J. Physiol. 122, 498-523. [12].

ERDMAN, W.J. and HEATHER, A.J. (1964). Objective measurement of spasticity by light reflection. Clin. Pharm. Therap. 5, No. 6, 883-886. [48].

ERLANGER, J. and GASSER, H.S. (1973). Electrical Signs of Nervous Activity. University of Pennsylvania Press, Philadelphia. [11].

FEATHER, N. (1963). An Introduction to the Physics of Vibrations and Waves. Edinburgh University Press, Edinburgh. [80].

FILIMONOFF, I.N. (1925). Klinische Beiträge zum Tonus problem. Ztschr. F.D. Ges. Neurol. U. Psychiat. 96, 368-421. [34, 35].

FINLAY, B. (1970). Dynamic mechanical testing of human skin "in vivo". J. Biomechanics. 3, 557-568. [77].

FOLEY, J. (1961). The stiffness of spastic muscle. J. Neurol., Neurosurg., Psychiat. 24, 125-131. [29].

FULTON, J.F. and PI-SUNER, J. (1927-28). A note concerning the probable function of various afferent end-organs in skeletal muscle. Amer. J. Physiol. 83, 554-562. [15].

GELFAN, S. (1963). Neurone and synapse populations in the spinal cord: indication of role in total integration. Nature 198, 162-165. [22].

GILDEMEISTER, M. (1914). Über die Sogenannte Härte Tierischer gewebe und ihre Messung. Ztschr. F. Biol. LXIII, 183-200. [32].

GOLDSCHEIDER, A. (1889). Untersuchungen über den Muskelsinn. Arch. Anat. Physiol. Lpz. 13, 369-502. [17].

GOLGI, C. (1903). Sui nervi dei tendini dell uomo e di altri vertebrati e di un nuovo organo nervoso terminale musculo tendineo. In: Opera Omnia Vol. I, 171-198. Hoepli, Milano. [15].

GOTCH, F. (1896). Note on the so-called tendon reflex. J. Physiol. 20, 322-333. [8].

GRANIT, R. (1966). Charles Scott Sherrington: An Appraisal. Nelson, London. [9, 11].

GRANIT, R. (1970). The Basis of Motor Control. Academic Press, London and New York. [12, 13, 14, 15].

GRANIT, R. (1972). Mechanisms Regulating the Discharge of Motoneurons. Liverpool University Press, Liverpool. [18, 24].

GRANIT, R. and HENATSCH, H.-D. (1956). Gamma control of dynamic properties of muscle spindles. J. Neurophysiol. 19, 356-366. [48].

GRANIT, R., HENATSCH, H.-D. and STEG, G. (1956). Tonic and phasic ventral horn cells differentiated by post-tetanic potentiation in cat extensors. Acta Physiol. Scand. 37, 114-126. [19].

GRANIT, R., HOLMGREN, B. and MERTON, P.A. (1955). The two roles for excitation of muscle and their subservience to the cerebellum. J. Physiol. 130, 213-224. [12].

GRANIT, R. and KAADA, B.R. (1952). Influence of stimulation of central nervous structures on muscle spindles in cat. Acta Physiol. Scand. 27, 130-160. [21].

GREGOR, A. and SCHILDRER, P. (1913). Zur psychophysiologie der muskel innervation. Ztschr. f.d. ges. Neurol. u. Psychiat. 18, 195-202. [45].

GRILLNER, S. (1972). The role of muscle stiffness in meeting the changing postural and locomotor requirements for force development by the ankle extensors. Acta Physiol. Scand. 86, 92-108. [28].

GRIMMER, R.V. and LANGWORTHY, O.R. (1941). An apparatus to record movement of the extremities. J. Lab. Clin. Med. 26, 1344-1347. [37].

GURFINKEL, V.S., LIPSHITS, M.I., MORI, S. and POPOV, K.E. (1975). Postural reactions to the controlled sinusoidal displacement of the supporting platform. Agressologie 17B, 71-76. [43].

HAGBARTH, K.-E. and EKLUND, G. (1966). Tonic vibration reflex (TVR) in spasticity. Brain Res. 2, 201-203. [48].

HALL, M. (1836). Lectures on the Nervous System. Sherwood, Gilbert and Piper, London. [5].

HALLIDAY, A.M. and REDFEARN, J.W.T. (1956). An analysis of the frequencies of finger tremor in healthy subjects. J. Physiol. 134, 600-611. [111].

HAMMOND, P.H. (1960). An experimental study of servo action in human muscular control. Proceedings of the Third International Conference on Medical Electronics, London. [43].

HAMMOND, P.H., MERTON, P.A. and SUTTON, G.G. (1956). Nervous gradation of muscular contraction. Brit. Med. Bull. 12, 214-218. [12].

HASSALL, A.H. (1849). The Microscopic Anatomy of the Human Body in Health and Disease. p. 345. Samuel Highley, London. [10].

HAY, J. (1901). Red and pale muscle. Liverpool Med.-Chir. J. 21, 431-451. [18].

HEIDENHAIN, R.P.H. (1856). Physiologische Studien. August Hirschwald, Berlin. [5].

HENNEMAN, E. (1974). Organization of the spinal cord. In: Medical Physiology. Ed. Mountcastle, V.B. C.V. Mosby, St. Louis. [18, 20].

HENNEMAN, E., SOMJEN, G. and CARPENTER, D.O. (1965a). Functional significance of cell size in spinal motoneurons. J. Neurophysiol. 28, 560. [19].

HENNEMAN, E., SOMJEN, G. and CARPENTER, D.O. (1965b). Excitability and inhibitability of motoneurons of different sizes. J. Neurophysiol. 28, 599. [19].

HERMAN, R. (1970). The myotatic reflex: clinico-physiological aspects of spasticity and contracture. Brain 93, 273-312. [25, 42.]

HERMAN, R., SCHAUMBURG, H. and REINER, S. (1967). A rotational joint apparatus. A device for study of tension-length relations of human muscle. Med. Res. Engng. 6, 18-20. [41].

HERMANN, L. (1879). Handbuch der Physiologie. Vol. I. F.C.W. Vogel, Leipzig. p. 9. [34].

HILL, A.V. (1951). A discussion on the thermodynamics of elasticity in biological tissues. Proc. Roy. Soc. B. 139, 464-497. [74].

HILL, D.K. (1968). Tension due to interaction between the sliding filaments in resting striated muscle. The effect of stimulation. J. Physiol. 199, 637-684. [27, 214, 215, 233].

HOEFER, P.F.A. and PUTNAM, T.J. (1939). Action potentials of muscles in normal subjects. Arch. Neurol. Psychiat. 42, 201-218. [45].

HOEFER, P.F.A. and PUTNAM, T.J. (1940A). Action potentials of muscles in "spastic" conditions. Arch. Neurol. Psychiat. 43, 1-22. [45].

HOEFER, P.F.A. and PUTNAM, T.J. (1940B). Action potentials of muscles in rigidity and tremor. Arch. Neurol. Psychiat. 43, 704-725. [45].

HOFFMAN, P. (1922). Untersuchungen Über Die Eigen Reflexe (Sehnen Reflexe) Menschlicher Muskeln. Springer, Berlin. [49].

HOLMES, G. (1952). Introduction to Clinical Neurology. E. & S. Livingstone Ltd., Edinburgh and London. [29].

HOLT, K.S. (1963). The measurement of muscle tone and posture. In: Cerebellum Posture and Cerebral Palsy. Ed. Walsh, E.G. Pp. 100-109. W. Heinemann. [44].

HUANG, C.R. (1976). Viscosity and viscoelasticity of blood systems. Thromb. Res. Suppl. II, 8, 1-8. [77].

HUFSCHMIDT, H. J. (1966). The stretch reflex in man and rabbit. J. Physiol. 185, 26-27P. [24].

HUNT, C.C. (1951). The reflex activity of mammalian small-nerve fibres. J. Physiol. 115, 456-469. [21].

HUNT, C.C. and PAINTAL, A.S. (1958). Spinal reflex regulation of fusimotor neurones. J. Physiol. 143, 195-212. [12].

HUNTER, J.I. (1925). The sympathetic innervation of striated muscle. B.M.J. I, pp. 197-201, 251-256, 298-301, 350-353, 398-403. [9].

INMAN, V.T., RALSTON, H.J., SAUNDERS, J.B. de C.M., FEINSTEIN, B. and WRIGHT, E.W. Jr. (1952). Relation of human electromyogram to muscular tension. Electroencephalog. and Clin. Neurophysiol. 4, 187-194. [45].

JACOBSON, E. and CARLSON. A.J. (1925). The influence of relaxation on the knee jerk. Am. J. Physiol. 73, 324-328. [48].

JANSEN, J.K.S. and RUDJORD, T. (1964). On the silent period and Golgi tendon organs of the soleus muscle of the cat. Acta Physiol. Scand. 62, 364-379. [15].

JOYCE, G.C., RACK, P.M.H. and ROSS, H.F. (1974). The forces generated at the human elbow joint in response to imposed sinusoidal movements of the forearm. J. Physiol. 240, 351-374. [40, 110].

JOYCE, G.C., RACK, P.M.H. and WESTBURY, D.R. (1969). The mechanical properties of cat soleus muscle during controlled lengthening and shortening movements. J. Physiol. 204, 461-474. [27].

KANDA, K. and RYMER, W.Z. (1977). An estimate of the secondary spindle receptor afferent contribution to the stretch reflex in extensor muscles of the decerebrate cat. J. Physiol. 264, 63-87. [24].

KIRKWOOD, P.A. and SEARS, T.A. (1974). Monosynaptic excitation of motoneurones from secondary endings of muscle spindles. Nature 252, 243-244. [24].

KNIGHT, D.E. (1975). Prospects for the printed motor. Engineering 215, No. 3, 199-202. [58].

KOBAYASHI, Y., OSHIMA, K. and TASAKI, I. (1952). Analysis of afferent and efferent systems in the muscle nerve of the toad and cat. J. Physiol. 117, 152-171. [21].

KÖLLIKER, A. (1863). Untersuchungen über die letzten endingungen der nerven. Z. Univ. Zool. 12, 149-164. [10].

KÜHNE, W. (1863). Die Muskelspindeln. Vitchow's Arch. path. Anat. 28, 528-538. [10].

KUNTZ, A. and KERKER, A.H. (1926). An experimental study of tonus in skeletal muscles as related to the sympathetic nervous system. Am. J. Physiol. 76, 121-143. [9, 35].

LA JOIE, W.J. and GERSTON, J.W. (1952). An objective method of evaluating muscle tightness. Arch. Phys. Med. 33, 595-603. [37].

LAPORTE, Y. and LLOYD, D.P.C. (1952). Nature and significance of reflex connections established by large afferent fibres of muscular origin. Am. J. Physiol. 169, 609-621. [114].

LAKIE, M. and TSEMENTZIS, S.A. (1979). Torque-resonance relationship at the wrist - a sex difference. J. Physiol. 295, 98-99P. [132].

LAKIE, M., WALSH, E.G. and WRIGHT, G.W. (1980). Thixotropy - a general property of the postural system. J. Physiol. 305, 73-74P. [171].

LEAVITT, L.A. and BEASLEY, W.C. (1964). Clinical application of quantitative methods in the study of spasticity. Clin. Pharm. Therap. 5, No. 6, 918-941. [39].

LEKSELL, L. (1945). The action potential and excitatory effects of the small ventral root fibres to skeletal muscle. Acta Physiol. Scand. 10, Suppl. 31. [11].

LEVINE, I.M. (Ed.). (1964). Symposium on skeletal muscle hypertonia. Clin. Pharm. Therap. 5, No. 6, part 2. [47].

LIDDELL, E.G.T. and SHERRINGTON, C.S. (1924). Reflexes in response to stretch (myotatic reflexes). Proc. Roy. Soc. B. 96, 212-242. [7, 25].

LINDSLEY, D.B. (1935). Electrical activity of human motor units during voluntary contraction. Am. J. Physiol. 114, 90-99. [45].

LINDSLEY, D.B. (1936). Electromyographic studies of neuromuscular disorders. Arch. Neurol. Psychiat. 36, 128-157. [45].

LIPPOLD, O.C.J. (1952). The relation between integrated action potentials in a human muscle and its isometric tension. J. Physiol. 117, 492-499. [30, 45].

LIPPOLD, O.C.J. (1970). Oscillation in the stretch reflex arc and the origin of the rhythmical, 8-12 c/s component of physiological tremor. J. Physiol. 206, 359-382. [111].

LITTLE CLUB memorandum on terminology and classification of cerebral palsy. Ed. Walsh, E.G. National Spastics Society Medical Education and Information Unit, London. [29].

LLOYD, D.P.C. (1941). The spinal mechanism of the pyramidal system in cats. J. Neurophysiol. 4, 525-540. [22].

LONG, C., THOMAS, D. and CROCHETIERE, W.J. (1964). Objective measurement of muscle tone in the hand. Clin. Pharm. Therap. 5, No. 6, 909-917. [39].

MACHIN, K.E. and PRINGLE, J.W.S. (1959). The physiology of insect fibrillar muscle. II. Mechanical properties of a beetle flight muscle. Proc. Roy. Soc. B 151, 204-225. [52, 75, 80].

MAGENDIE, F. (1823). Mémoire sur quelques découvertes récontes rélatives aux fonctions du system nerveux. Méquignon-Marvis, Paris. [6].

MAGLADERY, J.W., TEASDALL, R.D., PARK, A.M. and LANGUTH, H.W. (1952). Electrophysiological studies of reflex activity in patients with lesions of nervous system; comparison of spinal nervous system; comparison of spinal motoneurone excitability following afferent nerve volleys in normal persons and patients with upper motor neurone lesions. Bull. John Hopkins Hosp. 91, 219-244. [49].

MANGOLD, E. (1922). Untersuchungen über Muskel Härte. I. eine allgemein anwendbare Methode zur physiologischen Hartebestimmung. Arch. f.d. ges. Physiol. CXCVI, 200-214. II. dio Hartemessung in Totenstarre und Warmestarne. Arch. f.d. ges. Physiol. CXCVI, 215-228. [32].

MARSDEN, C.D., MERTON, P.A. and MORTON, H.B. (1976A). Servo action in the human thumb. J. Physiol. 257, 1-44. [13, 42, 59].

MARSDEN, C.D., MERTON, P.A. and MORTON, H.B. (1976B). Stretch reflex and servo action in a variety of human muscles. J. Physiol. 259, 531-560. [43].

MARTINEZ, N. (1966). Measurement of rigidity with a strain gauge myokinetograph. J. Neurosurg. 24, 315-316. [38].

MATTHEWS, B.H.C. (1933). Nerve endings in mammalian muscle. J. Physiol. 78, 1-33. [11, 12, 16].

MATTHEWS, P.B.C. (1959). A study of certain factors influencing the stretch reflex of the decerebrate cat. J. Physiol. 147, 547-564. [13].

MATTHEWS, P.B.C. (1969). Evidence that the secondary as well as the primary endings of the muscle spindles may be responsible for the tonic stretch reflex in the decerebrate cat. J. Physiol. 204, 365-393. [24].

MATTHEWS, P.B.C. (1972). Mammalian muscle receptors and their central actions. Arnold, London. [13, 24].

MATTHEWS, P.B.C. and RUSHWORTH, G. (1957). The selective effect of procaine on the stretch reflex and tendon jerk of soleus muscle when applied to its nerve. J. Physiol. 135, 246-262. [16].

MCKINLEY, J.C. and BERKWITZ, N.J. (1928). Quantitative studies on human muscle tonus. I. Description of methods. Arch. Neurol. Psychiat. 19, 1036-1056. [34, 35].

MERTON, P.A. (1953). Speculations on the servo-control of movement. In: The Spinal Cord. Ciba Symposium. Pp. 247-260. Churchill, London. [12].

MILLER, D.I. and MORRISON, W.E. (1975). Prediction of segmental parameters using the Hanavan human body model. Med. Sci. Sports 7, No. 3, 207-212. [109].

MITCHELL, S.W. and LEWIS, M.J. (1886). Physiological studies of the knee-jerk, and of the reactions of muscles under mechanical and other excitants. Med. News Phila. X/VIII, 169-173. [47].

MORITANI, T. and de VRIES, H.A. (1978). Re-examination of the relationship between the surface integrated electromyogram (I.E.M.G.) and force of isometric contraction. Am. J. Phys. Med. 57, No. 6, 263-277. [30].

MOSSO, A. (1896). Description d'un myotonomètre pour études la tonicité des muscles chez l'homme. Arch. Ital. de Biol. 25, 349-384. [32].

MOTT, F.W. and SHERRINGTON, C.S. (1895). Experiments upon the influence of sensory nerves upon movement and nutrition of the limbs. Proc. Roy. Soc. B 57, 481-488. [7].

MÜLLER, J. (1842). Physiology. Trans. Baly, W. Taylor and Walton, London. A translation of the 1840 edition. [4].

NASHOLD, B.S. (1966). An electronic method of measuring and recording resistance to passive muscle stress. J. Neurosurg. 24, 310-314. [38].

NEEDHAM, D. (1971). Machina Carnis; the biochemistry of muscular contraction and its historical development. Cambridge University Press, London. [17].

NICHOLS, T.R. and HOUK, J.C. (1976). Improvement in linearity and regulation of stiffness that results from actions of stretch reflex. J. Neurophysiol. 39, 119-142. [24, 27, 215].

NÖEL, G. (1973). In: New Developments in Electromyography and Clinical Neurophysiology. Ed. J.E. Desmedt. Vol. 3, 15-19. Karger, Basel. [5].

NOYONS, A. and von UEXHILL, J. (1911). Die härte der Muskeln. Ztschr. F. Biol. LVI, 139-208. [32].

PASKIND, H.A. (1932). The effect of laughter on muscle tone. Arch. Neurol. Psychiat. 28, 623-628. [5, 36].

PETEKFI, T. (1927). Die abhebung der befructungsmembran bei seeigeleiern. Arch. fur Entwicklungs Mechanic 112, 660-695. [217].

PIPER, H. (1907). Über den willkürlichen muskeltetanus. Arch. f.d. ges. Physiol. CXIX, 301-338. [44].

POLÁČEK, P. (1966). Receptors of the joint. Acta Facult. Med. Univ. Brno. 23, 107 pp. [15].

POLLOCK, L.J. (1928). Muscle tone. J.A.M.A. 91, 221-223. [5, 25].

POLLOCK, L.J. and DAVIS, L. (1932). Reaction of modifications of muscle tonus to interruption of certain anatomic pathways. Arch. Neurol. Psychiat. 28, 586-602. [36].

RACK, P.M.H. and WESTBURY, D.R. (1974). The short range stiffness of active mammalian muscle and its effect on mechanical properties. J. Physiol. 240, 331-350. [27, 215].

RALSTON, H.J. and LIBET, B. (1953). The question of tonus in skeletal muscle. Am. J. Phys. Med. 32, 85-92. [22, 46].

RAMÓN y CAJAL, S. (1909). Histologie du Système de l'homme et des Vertébrés. A. Maloine, Paris. [19].

RANDALL, J.E. and STILES, R.N. (1964). Power spectral analysis of finger acceleration tremor. J. appl. Physiol. 19, 357-360. [111].

RANSON, S.W. (1928). The role of the dorsal roots in muscle tonus. Arch. Neurol. Psychiat. 19.2, 201-241. [9].

RANVIER, L. (1874). De quelques faits relatifs à l'histologie et à la physiologie des muscles striés. Arch. Physiol. Norm. Pathol. 6, 1-15. [17].

REXED, B. (1944). Contributions to the knowledge of the post-natal development of the peripheral nervous system in man. Acta Psychiat. Neurol. Suppl. 33. [18].

ROBERTS, T.D.M. (1963). Rhythmic excitation of a stretch reflex revealing (A) hysteresis and (B) a difference between the responses to pulling and to stretching. Q. J. exp. Physiol. 197, 328-345. [30, 52, 53].

RONPOT, P. and METRAL, S. (1973). Analysis of shortening reaction in man. In: New Developments in Electromyography and Clinical Neurophysiology, Vol. 3. Ed. J.E. Desmedt. Karger, Basel. [114].

RONPOT, P. and SCHERRER, J. (1966). Contraction réflexe provoquée par le raccourcissement passif du muscle dans l'athétose et les dystonies d'attitudes. Rev. Neurol. (Paris) 114, 329-337. [114].

ROSSI, G. (1927). Asimmetrice toniche posturale, ed asimmetrie motorie. Arch. Fisiol. 25, 146-157. [11].

ROTHWELL, N.J. and STOCK, M.J. (1979). A role for brown adipose tissue in diet-induced thermogenesis. Nature 281, 31-35. [223].

RUFFINI, A. (1898). On the minute anatomy of the neuro-muscular spindles of the cat, and on their physiological significance. J. Physiol. 23, 190-208. [10].

SALMONS, S. and VRBOVÁ, G. (1967). Changes in the speed of mammalian fast muscle following long-term stimulation. J. Physiol. 192, 39-40P. [18].

SCHALTENBRAND, G. (1929). Muscle tone in man. Arch. surg. 18, 1874-1885. [36].

SCHMIDT, R.F. (1978). Fundamentals of Neurophysiology. Springer-Verlag, New York, Heidelberg, Berlin. [22, 223].

SCHWAB, R.S. (1963). Evaluation and correlations of the Wartenburg swing tests in Parkinson's Disease. Tr. Am. Neurol. A. 88, 270-274. [44].

SCHWAB, R.S. (1964). Clinical estimation of rigidity. Clin. Pharm. Therap. 5, No. 6, 942-946. [44].

SHAW, J.C. (1967). Integration techniques. In: A Manual of Psychophysiological Methods. Ed. Venables, P.H. and Martin, I. North Holland Publishing. [47].

SHERRINGTON, C.S. (1893). Experiment in examination of the peripheral distribution of the fibres of the posterior roots of some spinal nerves. Proc. Roy. Soc. lii, 333-337. [7].

SHERRINGTON, C.S. (1894). On the anatomical constituents of nerves of skeletal muscle; with remarks on recurrent fibres in the ventral spinal nerve-root. J. Physiol. 17, 211-258. [7, 11].

SHERRINGTON, C.S. (1900). In: Textbook of Physiology, Vol. 2, 799-800. Ed. E.A. Schäfer. Young J. Pentland, Edinburgh and London. [7].

SHERRINGTON, C.S. (1906). The Integrative Action of the Nervous System. Yale University Press, New Haven. [8, 9].

SHERRINGTON, C.S. (1909). On plastic tonus and proprioceptive reflexes. Q. J. exp. Physiol. 2, 109-156. [8].

SHERRINGTON, C.S. (1913). Reflex inhibition as a factor in the co-ordination of movements and postures. Q. J. exp. Physiol. 6, 251-310. [8].

SHERRINGTON, C.S. (1940). Man on his Nature. Cambridge University Press. [3].

SMITH, A.E., MARTIN, D.S., GARVEY, P.H. and FENN, W.O. (1930). A dynamic method for measurement of muscle tonus in man. J. Clin. Invest. 8, 597-622. [31, 36].

SMITH, O.C. (1934). Action potentials from single motor units in voluntary contraction. Am. J. Physiol. 108, 629-638. [45].

SPIEGEL, E.A. (1923). Zur Physiologie und Pathologie des Skeletmuskel tonus. Ztschr. f.d. ges. Neurol. U. Psychiat. 81, 517-624. [34, 35].

SPRINGER, R. (1914). Untersuchungen über die Resistenz (die sogenannte härte) menschlicher Muskeln. Ztschr. F. Biol. LXIII, 200-222. [32].

STILES, R.N. and RANDALL, J.E. (1967). Mechanical factors in human tremor frequency. J. appl. Physiol. 23, 324-330. [111].

STONE, S.L., THOMAS, J.G. and ZAKIAN, V. (1965). The passive rotatory characteristics of the dog's eye and its attachments. J. Physiol. 181, 337-349. [211].

SUCH, C.H., UNSWORTH, A., WRIGHT, V. and DOWSON, D. (1975). Quantitative study of stiffness in the knee joint. Ann. Rheum. Dis. 34 (4), 286-291. [166].

THOMPSON, D.T. (1978). A study of Knee Joint Stiffness. Ph.D. Thesis, Leeds University. [108, 167].

THOMSON, W.T. (1964). Mechanical Vibrations. Allen and Unwin, London. [80].

TIEDMANN, F. (1834). A systematic treatise on comparative physiology, introductory to the physiology of man. Volume I. Trans. J.M. Gully and J.H. Lane. John Churchill, London. [4].

TIMBERLAKE, W.H. (1964). Evaluation of hypertonia with the use of a gravity-driven ergograph. Clin. Pharm. Therap. 5, 879-882. [39].

TODD, R.B. (1847). Cyclopedia of Anatomy and Physiology. Sherwood, Gilbert and Piper, London. [2].

TSCHIRIEW, S. (1879). Tonus querfestreifter Muskeln. Arch. f. Physiol. (Leipzig), 78-89. [5].

TSEMENTZIS, S.A., GILLINGHAM, F.J., GORDON, A. and LAKIE, M.D. (1980). Two methods of measuring muscle tone applied in patients with decerebrate rigidity. J. Neurol., Neurosurg., Psychiat. 43, 25-36. [134].

WALSH, E.G. (1968). Oscillations of the head, trunk and limbs induced by mechanical means. J. Physiol. 198, 69-72P. [52].

WALSH, E.G. (1973). Motion at the wrist induced by rhythmic forces. J. Physiol. 230, 44-45P. [52, 132].

WALSH, E.G. (1975a). Resonance at the wrist - a "jump" effect. J. Physiol. 245, 69-70P. [123].

WALSH, E.G. (1975b). Jump effect at the wrist - model using light or non-linear damping. J. Physiol. 248, 19-20P. [123].

WALSH, E.G. (1975c). Feed-back induced muscular exercise. J. Physiol. 251, 6-7P. [52, 127].

WARTENBURG, R. (1951). Rarely used neurologic tests. Tr. Am. Neurol. A. 76, 255-256. [44].

WEBSTER, D.D. (1959). A method of measuring the dynamic characteristics of muscle rigidity, strength, and tremor in the upper extremity. Med. Electronics 6, 159-164. [38].

WEBSTER, D.D. (1964). The dynamic quantitation of spasticity with automated integrals of passive motion resistance. Clin. Pharm. Therap. 5, No. 6, 900-908. [38].

WEBSTER, D.D. (1966). Rigidity in extrapyramindal disease. J. Neurosurg. 24, 299-309. [38].

WESTPHAL, C.F.O. (1877). Unterschenkel phänomen und Nervendehung. Arch. Psychiat. Nervenkr. 7, 666-670. [114].

WIENEKE, G.H. (1972). Variations in the output impedance of the human motor system. Ph.D. Thesis, State University, Utrecht. [43].

WRIGHT, V. and JOHNS, R.J. (1960). Quantitative and qualitative analysis of joint stiffness in normal subjects and in patients with connective tissue disease. Ann. Rheumat. Dis. 20, 36-46. [39, 167].

WUNDT, W. (1858). Die lehre von der muskelbewegung nach eigenen untersuchungen bearbitet. Freidrch Bieweg & Son, Braunsweig. [5].

APPENDIX: Relevant published papers.

[*From the Proceedings of the Physiological Society*, 22–23 *June* 1979
Journal of Physiology, **295**, 98–99*P*]

Wrist compliance

By M. Lakie*, E. G. Walsh and G. Wright. *Department of Physiology, Medical Buildings, Teviot Place, Edinburgh EH8 9AG*

When sinusoidal forces varying between 1 and 20 Hz are imparted to the wrist a resonance is seen which rises in frequency if the torque is reduced below a critical value (Walsh, 1973; Lakie & Tsementzis, 1979). This rise indicates that the system is stiffer for small as compared with large movements. We have now measured the wrist compliance of eight relaxed subjects more directly.

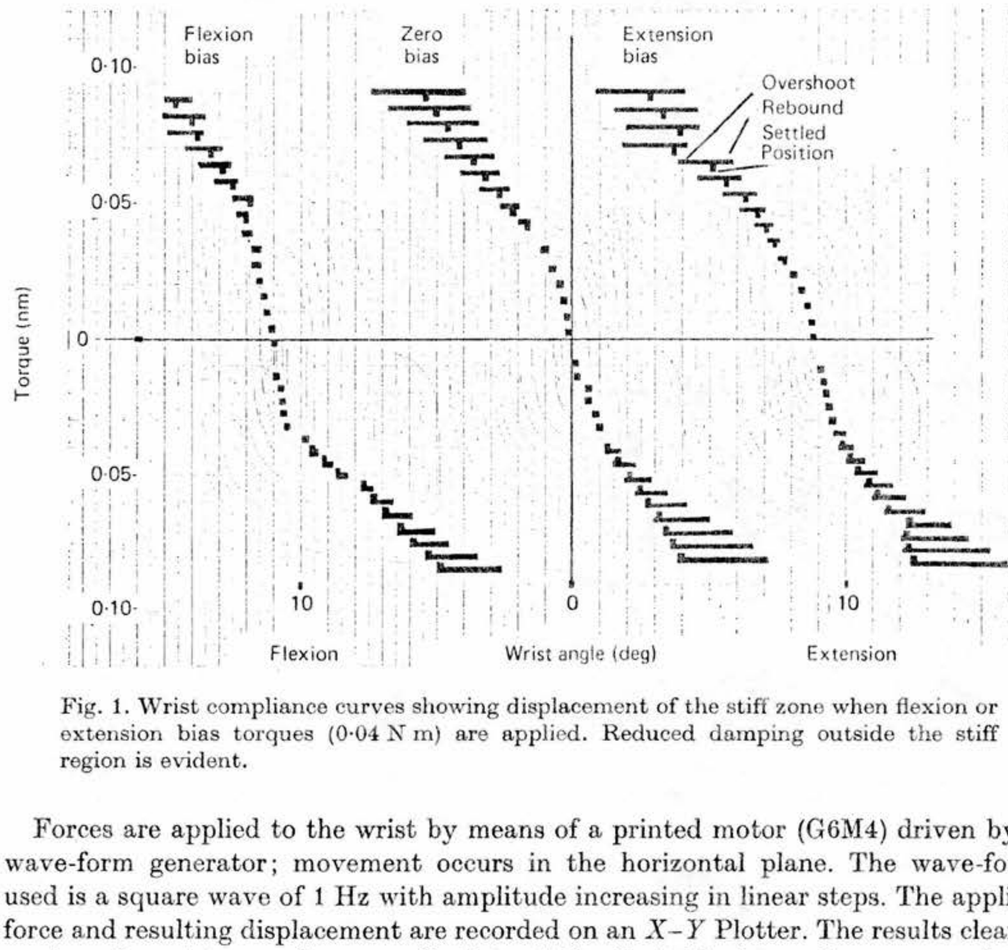

Fig. 1. Wrist compliance curves showing displacement of the stiff zone when flexion or extension bias torques (0·04 N m) are applied. Reduced damping outside the stiff region is evident.

Forces are applied to the wrist by means of a printed motor (G6M4) driven by a wave-form generator; movement occurs in the horizontal plane. The wave-form used is a square wave of 1 Hz with amplitude increasing in linear steps. The applied force and resulting displacement are recorded on an X–Y Plotter. The results clearly confirm the existence of a zone of substantially diminished compliance around the position of rest (Fig. 1). When a continuous biasing current is, additionally, fed to the motor, the stiff region is displaced to the new position of rest. Friction in the joint, or more probably in the muscles or tendons, seems to be the probable cause of the stiffness for small displacements. Overshoot and sometimes also rebound occurs before equilibrium is reached in the compliant zone but not in the central stiff zone; it is evident that there also the damping is significantly greater.

REFERENCES

Lakie, M., Tzementzis, S. A. (1979). *J. Physiol.* **289**, 86*P*.
Walsh, E. G. (1973). *J. Physiol.* **230**, 44–45*P*.

* M.R.C. student.

[*From the Proceedings of the Physiological Society*, 13–14 *July* 1979
Journal of Physiology, **296**, 47–48*P*]

Cooling and wrist compliance

By M. Lakie*, E. G. Walsh and G. W. Wright. *Department of Physiology, University Medical School, Teviot Place, Edinburgh EH8 9AG*

People who are cold often complain of muscular stiffness and cooling is said to increase muscle tone. We have investigated these claims using a wrist compliance measuring method (Lakie, Walsh & Wright, 1979). Pulses of force lasting 1·0 s that changed in a linear stepwise manner were applied to the hand from a small printed motor and the resultant motion recorded.

Subjects had an arm cooled by water at 2 °C for 20 min. Final skin temperature was about 5 °C. In one group the limb below the elbow was cooled, in the other only the hand and wrist. A control compliance curve was plotted for each subject immediately prior to cooling. E.m.g. records were taken and consisted mainly of transient shortening reactions.

Forearm cooling caused a considerable increase in stiffness (Fig. 1). There was a concurrent substantial decrease in e.m.g. activity. Hand and wrist cooling did not affect either stiffness or the e.m.g. Neither procedure caused any changes in the opposite arm.

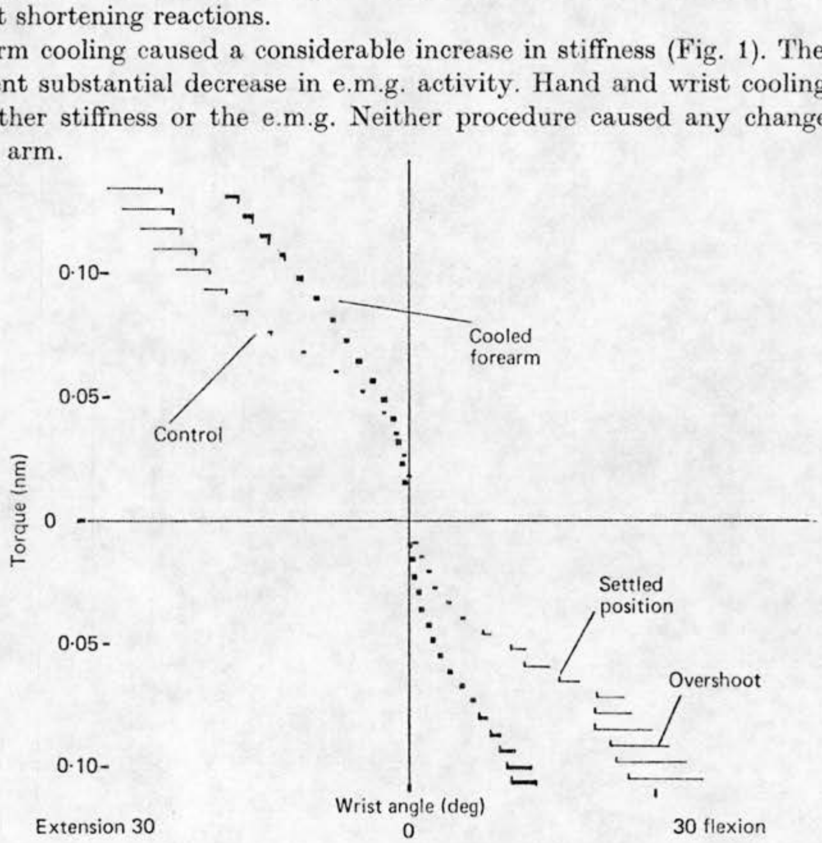

Fig. 1. Right wrist compliance before and after forearm cooling. Subject L.R., aet 22, female.

Cooling causes a decreased compliance probably by a direct action on muscle and this is accompanied by a decreased e.m.g.

REFERENCE

Lakie, M., Walsh, E. G. & Wright, G. W. (1979). *J. Physiol.* **295**, 98–99*P*.

* M.R.C. Postgraduate student.

[*From the Proceedings of the Physiological Society*, 2–3 *November* 1979
Journal of Physiology, **300**, 36–37*P*]

Passive wrist movements – a large thixotropic effect

By M. Lakie*, E. G. Walsh and G. Wright. *Department of Physiology, University of Edinburgh, Teviot Place, Edinburgh EH8 9AG*

The relaxed wrist is much stiffer for small than for large movements (Lakie, Walsh & Wright, 1979). We now believe that this effect is due to thixotropy. A large thixotropic effect may be shown if the wrist is oscillated in the horizontal plane by small low-frequency (e.g. 2·5 Hz) sinusoidal or rectangular torques provided by a (G6M4) printed motor, for the extent of the motion obtained may be heavily dependent on previously applied greater forces. If after the small force is applied a larger perturbation is introduced for one or more cycles, the amplitude of the motion thereafter may be increased several-fold (Fig. 1). This increased flexibility can continue indefinitely. If the driving force is now cut out for (say) 2 sec and then reapplied, the motion is reduced to its original level. During these procedures the e.m.g. is usually silent. With slow square torques (1·0 Hz) the effect is also seen; the motion may double and the overshoots are reduced and sometimes abolished.

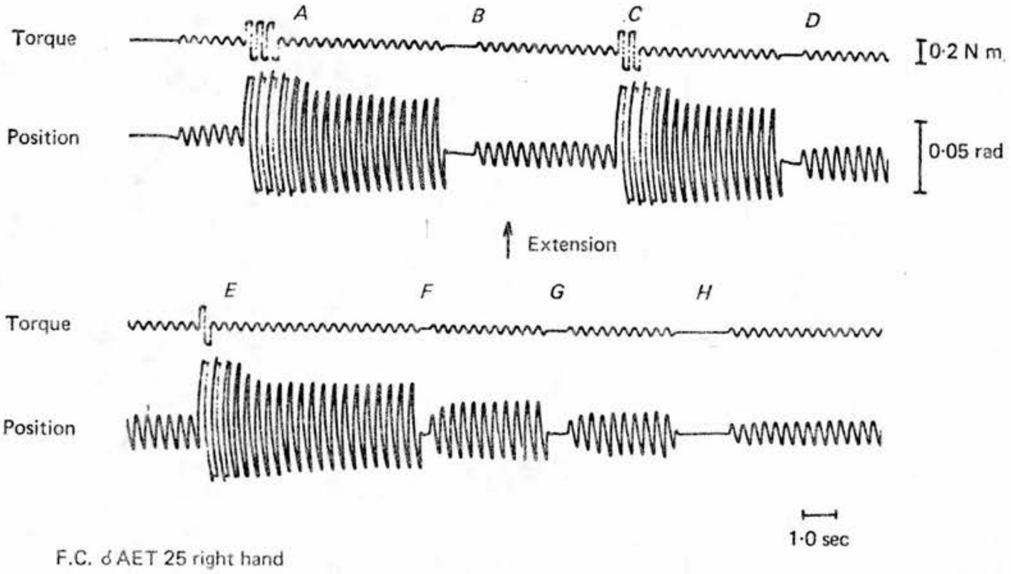

Fig. 1. *A*, *C* and *E*, large perturbations of 3, 2 and 1 cycle respectively cause same increase in amplitude. *B*, *D*, *F*, *G* and *H*, driving force is cut out for 3, 2, 1, 2 and 4 cycles respectively. Three or four cycles (*B* and *H*) cause reduction in amplitude to original level; less than three cycles (*D*, *F* and *G*) cause partial reduction. All changes can be prolonged indefinitely.

Active movements also may be equally effective in loosening the system. Thixotropy may be of considerable assistance to the nervous system by reducing small postural perturbations.

REFERENCE

Lakie, M., Walsh, E. G. & Wright, G. (1979). *J. Physiol.* **295**, 98–99*P*.

* M.R.C. postgraduate student.

[*From the Proceedings of the Physiological Society*, 17–18 *December* 1979
Journal of Physiology, **301**, 23 *P*]

Anaesthesia does not (and cannot) reduce muscle tone?

BY M. LAKIE*, S. T. TSEMENTZIS, E. G. WALSH and G. WRIGHT. *Departments of Physiology and Surgical Neurology, Edinburgh University*

Passive movements of the wrist caused by forces from a (G6M4) printed motor have been recorded in 14 patients anaesthetized with a mixture of volatile and intravenous anaesthetics and treated with (so-called) muscle relaxants (Fig. 1). In eight patients, low amplitude sinusoidal torques (e.g. 0·1 N m) at low frequency (e.g. 2·5 Hz) have been used. As compared with the pre-anaesthetic state there has been no change in the amplitude of the movements. The thixotropic effect (Lakie, Walsh

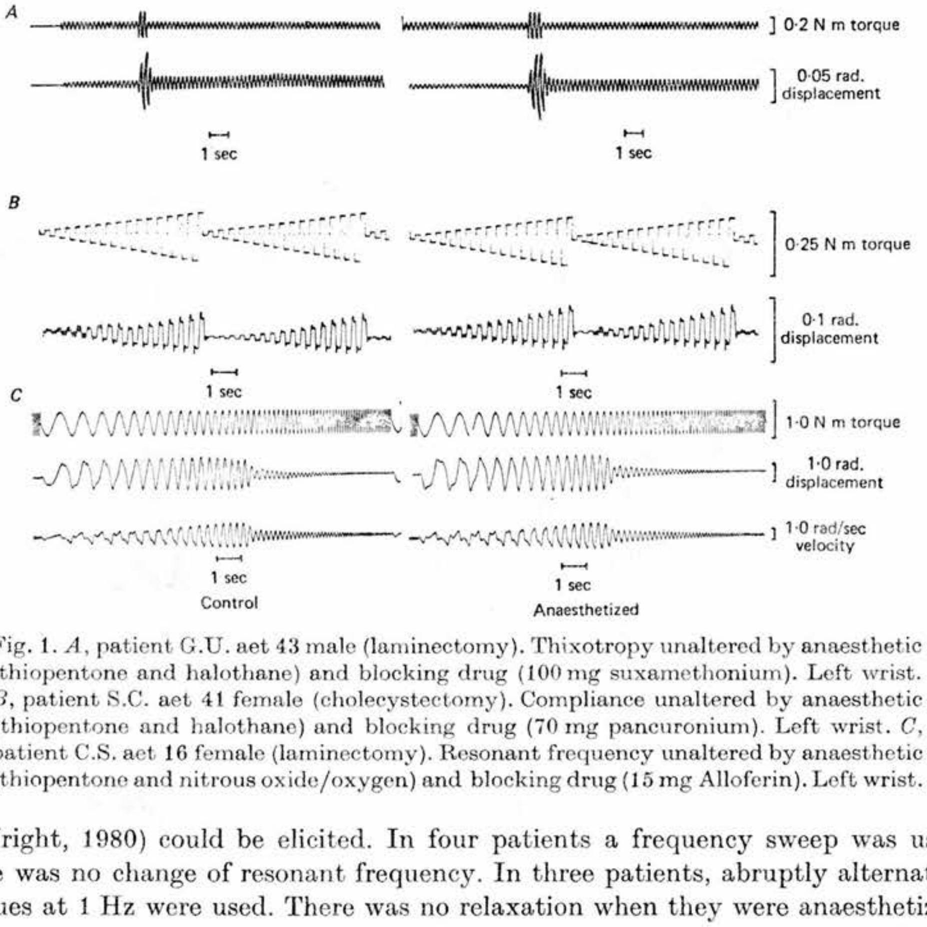

Fig. 1. *A*, patient G.U. aet 43 male (laminectomy). Thixotropy unaltered by anaesthetic (thiopentone and halothane) and blocking drug (100 mg suxamethonium). Left wrist. *B*, patient S.C. aet 41 female (cholecystectomy). Compliance unaltered by anaesthetic (thiopentone and halothane) and blocking drug (70 mg pancuronium). Left wrist. *C*, patient C.S. aet 16 female (laminectomy). Resonant frequency unaltered by anaesthetic (thiopentone and nitrous oxide/oxygen) and blocking drug (15 mg Alloferin). Left wrist.

& Wright, 1980) could be elicited. In four patients a frequency sweep was used, there was no change of resonant frequency. In three patients, abruptly alternating torques at 1 Hz were used. There was no relaxation when they were anaesthetized. In four patients compliance curves were plotted (e.g. Lakie, Walsh & Wright, 1979) there were no changes in three of these.

It is concluded that general anaesthesia and muscle relaxants do not reduce the muscle tone of the forearm below the basal level found in a relaxed conscious subject.

REFERENCES

LAKIE, M., WALSH, E. G. & WRIGHT, G. (1979). *J. Physiol.* **295**, 98*P*.
LAKIE, M., WALSH, E. G. & WRIGHT, G. (1980). *J. Physiol.* **300**, 36–37*P*.

* M.R.C. Student.

[*From the Proceedings of the Physiological Society*, 28–29 *March* 1980
Journal of Physiology, **305**, 73–74*P*]

Thixotropy – a general property of the postural system

By M. Lakie*, E. G. Walsh and G. W. Wright. *Department of Physiology, University Medical School, Teviot Place, Edinburgh EH8 9AG*

A thixotropic substance has a viscosity which can be reduced temporarily by stirring. Stirring disrupts weak intermolecular bonds and these bonds can take some time to reform.

We recently described a large thixotropic effect at the wrist (Lakie, Walsh & Wright, 1980). When this joint was subjected to small rhythmic forces the movements obtained were increased several-fold by a transient larger perturbation.

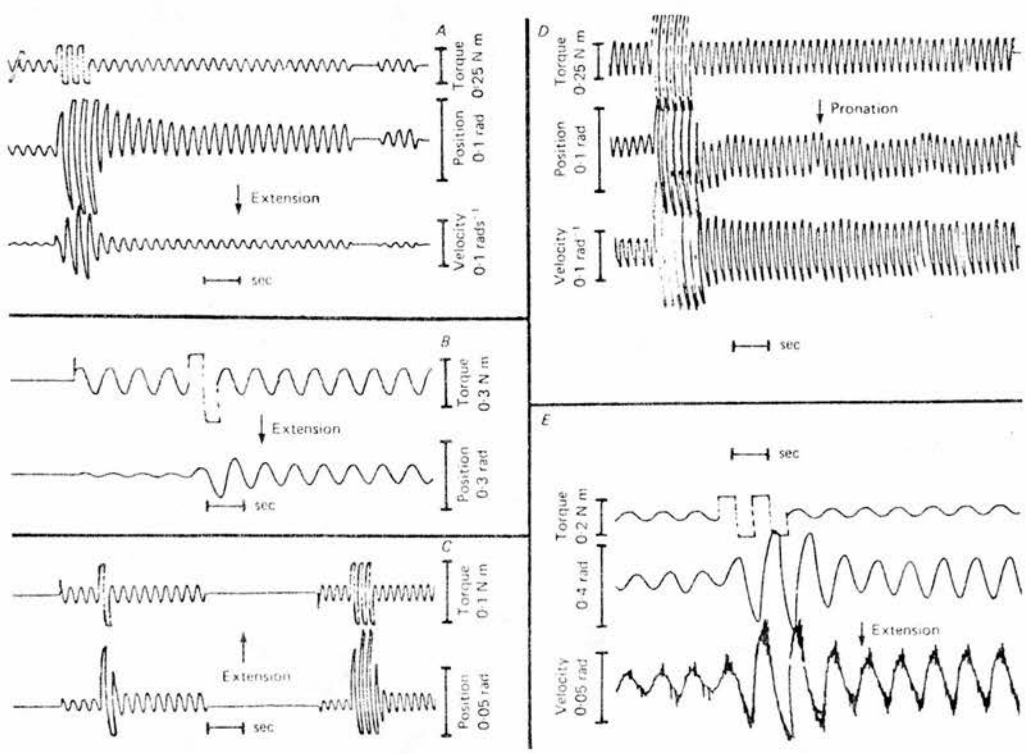

Fig. 1. *A*, flexion/extension of right ankle. *B*, flexion/extension of right knee. *C*, flexion/extension of left index finger proximal interphalangeal joint. *D*, pronation/supination of right forearm. *E*, flexion/extension of right elbow.

We have now examined other parts of the body with suitably modified apparatus. Thixotropic effects have been seen for flexion/extension movements of the elbow, knee and ankle, a proximal interphalangeal joint and a metacarpo-phalangeal joint, for pronation and supination movements of the forearm and for elevation and depression of the jaw (Fig. 1).

When rhythmic forces are applied by a lever to the tendon of the biceps femoris the muscle can be rhythmically stretched without moving the knee. An active or passive movement of the knee may then increase the subsequent motion of the tendon substantially. Accordingly a major component of the thixotropy lies in the muscle and possibly corresponds to the 'short range elastic component of muscle stiffness' described by Hill (1968).

REFERENCES

Lakie, M., Walsh, E. G. & Wright, G. W. (1980). *J. Physiol.* **300**, 36*P*.
Hill, D. K. (1968). *J. Physiol.* **199**, 637–684.

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[*From the Proceedings of the Physiological Society*, 10–11 *July* 1980
Journal of Physiology, **308**, 40–41*P*]

Damping at the wrist – a sex difference

BY M. LAKIE*, E. G. WALSH and G. WRIGHT. *Department of Physiology, University of Edinburgh, Teviot Place, Edinburgh EH8 9AG*

When a sinusoidally varying force at an appropriate frequency is applied to the relaxed wrist, a resonance occurs because of the interaction of elastic and inertial elements in the system (Walsh, 1973). At resonance the velocity and amplitude are limited only by the viscous and frictional components (damping) in the system.

The peak velocity and peak amplitude of the resonating wrist have been measured at seven different levels of torque in 11 male and 12 female subjects. Both wrists were tested. The results are summarized in Fig. 1.

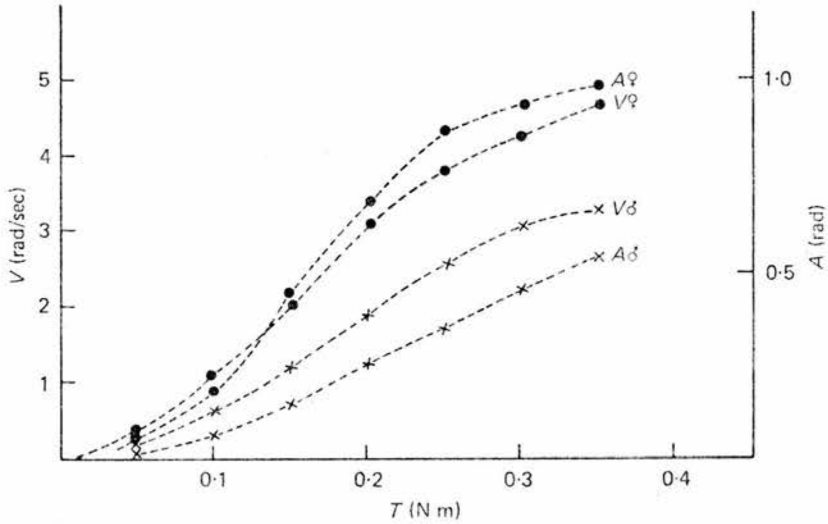

Fig. 1. Peak velocity (V) and peak amplitude (A) of resonating wrist at seven levels of torque (T). The values of V and A are the means of twenty-four female wrists and twenty-two male wrists. The sex difference for V and for A is significant ($P < 0{\cdot}01$). There is no significant difference between left and right wrists.

Two observations can be made.

(1) The damping is non-linear, being greater for small torques. We believe that this is caused by thixotropy in the muscles (Lakie, Walsh & Wright, 1979*b*) and accounts for the non-linear compliance curve of the wrist (Lakie, Walsh & Wright, 1979*a*).

(2) At all levels of torque the damping is considerably less in female subjects; this is probably due to a smaller bulk of muscle. It has previously been shown that the resonant frequency rises rapidly if the driving torque is reduced below a critical level, and the critical level is greater for men than women (Lakie & Tsementzis, 1979). We now think that the higher critical level is a reflection of greater bulk of male muscles.

* M. Lakie is supported by a grant from the Chest, Heart and Stroke Association.

REFERENCES

LAKIE, M., WALSH, E. G. & WRIGHT, G. W. (1979*a*). *J. Physiol.* **295**, 98–99*P*.
LAKIE, M., WALSH, E. G. & WRIGHT, G. W. (1979*b*). *J. Physiol.* **300**, 36–37*P*.
LAKIE, M. & TSEMENTZIS, S. A. (1979). *J. Physiol.* **289**, 86*P*.
WALSH, E. G. (1973). *J. Physiol.* **230**, 44–45*P*.

[*From the Proceedings of the Physiological Society*, 12 *September* 1980
Journal of Physiology, **310**, 3–4*P*]

Measurements of inertia of the hand, and the stiffness of the forearm muscles using resonant frequency methods, with added inertia or position feedback

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The hand, supported to flex and extend in a horizontal plane, behaves as a slightly underdamped torsion pendulum with a resonant frequency (f_0) demonstrable by the use of rhythmic torques: Fig. 1 (Walsh, 1973; Lakie & Tsementzis, 1979).

The resonant frequency can be lowered (to f_B) by fixing a bar of metal (inertia J_B) to the system. The inertia of the hand (J_0) is given by

$$J_0 = J_B \frac{(f_B)^2}{(f_0)^2 - (f_B)^2}.$$

It is desirable to correct for the inertia (0·6 g m²) of the apparatus. Negative position feedback can increase the stiffness by a factor K_F; the new resonant frequency f_F is higher than f_0. With positive position feedback K_F is negative and f_F is lower than f_0. Muscle stiffness K_0 is given by

$$K_0 = K_F \frac{(f_0)^2}{(f_F)^2 - (f_0)^2}.$$

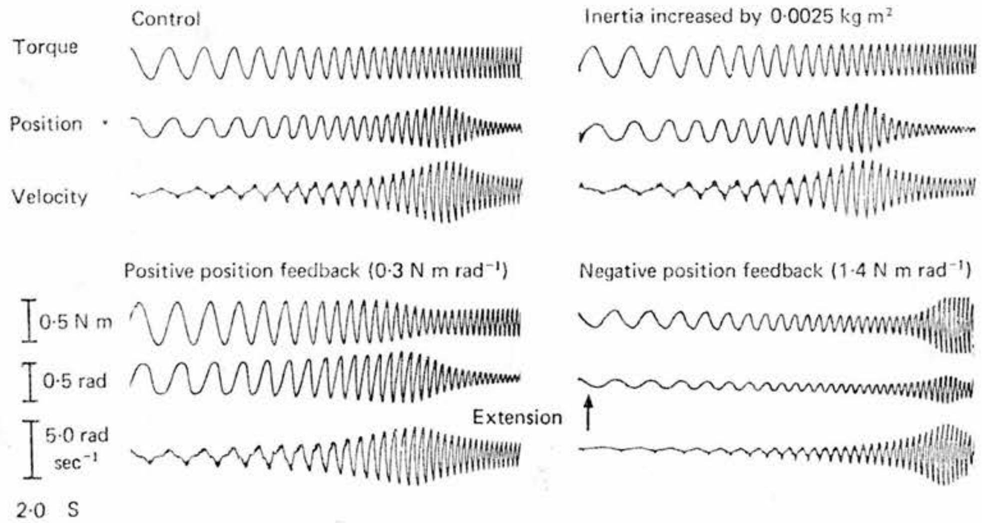

Fig. 1. Top left, no added inertia, no feedback. Frequency sweep demonstrates resonance at 2·78 Hz (f_0). Top right, added inertia f_B = 2·21 Hz. Bottom left, positive feedback $-f_F$ = 2·44 Hz. Bottom right, negative feedback $-f_F$ = 4·7 Hz. From these observations the calculated values for the inertia of the hand are 3·7, 3·4 and 3·1 g m² respectively. The calculated values for muscle stiffness using the three methods are 1·23, 1·22 and 1·12 N m rad⁻¹ respectively. Considerable passive tension evidently develops. Thus with a hand displacement of 1·0 rad (assuming tendons are 1·5 cm from axis) the force in the stretched muscles is about 80 N. [M.L. aet 26♂ right wrist.]

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The formula for a torsion pendulum

$$f_0 = \frac{1}{2\pi}\sqrt{\frac{K_0}{J_0}}$$

gives the stiffness of the muscles if the inertia has been determined, and vice versa.

For sensible results the torques must not be so small that thixotropy is significant (Lakie, Walsh & Wright, 1980) nor so large that reflex muscular reactions are induced. With positive position feedback the toggle action (negative stiffness) must be less than K_0 or the system is no longer resonant.

REFERENCES

LAKIE, M. & TSEMENTZIS, S. A. (1979). *J. Physiol.* **289**, 86*P*.

LAKIE, M., WALSH, E. G. & WRIGHT, G. (1980). *J. Physiol.* **300**, 36–37*P*.

WALSH, E. G. (1973). *J. Physiol.* **230**, 44–45*P*.

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Sudden increase of wrist stiffness for small movements – demonstrated by positive velocity feedback

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A low-friction printed motor is coupled to the wrist and provided with a tachometer, the output of which is squared, then modulated to increase or decrease linearly, and fed to the motor-drive amplifier. With positive velocity feedback (Walsh, 1969) there is negative damping and the system oscillates at its resonant frequency (Fig. 1). With higher torques the frequency is essentially constant; the system is linear. As the force falls the rate abruptly increases; the wrist becomes at least twice as stiff (cf. Walsh, 1972; Lakie & Tsementzis, 1979). The change of frequency occurs at a clearly lower force level as the force is falling than when it is rising, evidently a thixotropic effect (cf. Lakie, Walsh & Wright, 1980*a*).

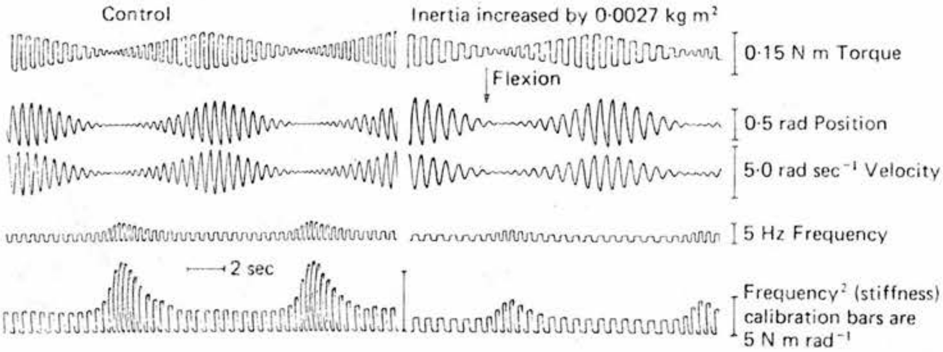

Fig. 1. Subject M.A.L. ♀ aet 26 right wrist. The interrelationship of torque and resonant frequency is shown. The stiffness of the system is proportional to the frequency squared; the stiffness has been calibrated by the addition of extra inertia (for method see Lakie, Walsh & Wright, 1980*b*). The stiffness rises abruptly at a low torque level as the force wanes, reaches a maximum which does not coincide with the lowest torque, and decreases gradually as torque increases. This highly asymmetrical behaviour provides clear evidence of thixotropy in the system. With additional inertia the same pattern is seen, but at a reduced frequency.

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REFERENCES

LAKIE, M. & TSEMENTZIS, S. A. (1979). *J. Physiol.* **289**, 86*P*.
LAKIE, M., WALSH, E. G. & WRIGHT, G. (1980*a*). *J. Physiol.* **300**, 36–37*P*.
LAKIE, M., WALSH, E. G. & WRIGHT, G. (1980*b*). *J. Physiol.* (in the Press).
WALSH, E. G. (1969). *J. Physiol.* **207**, 16–17*P*.
WALSH, E. G. (1972). *J. Physiol.* **230**, 44–45*P*.