

THE PSYCHO-PHYSIOLOGY OF THE PHASIC
STRETCH REFLEX

Alex. M. Clarke

This statement is to certify that the
experiments described in this thesis
were my own original work.

This thesis was submitted in partial
fulfilment of the requirements for
the degree of Doctor of Philosophy in
The Australian National University

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ERRATA

- Page 51. Third line should read "... ratio of 200/1 ..."
- Page 53. Third paragraph should read "... placed 9.5 cm apart over the belly ..."
- Page 59. First line should read "... so that ..."
- Page 78. Line 14 should read "... the rate of extension determines ..."
- Page 91. First line should read "... efferent fibres ..."
- Page 105. Third line should read "... cause any significant augmentation of the response."
- Page 106. DISCUSSION. First paragraph, line 5 should read "... the response is mostly not significantly affected ..."
- Page 109. Second paragraph, line 6 should read "... did not produce significant facilitation."
- Page 124. Last paragraph, line 5 should read "... there was no significant difference in mean impulse of the MAP ..."
- Page 136. Last paragraph of the section sub-titled The effect of 3 clicks on the dependent variables should read "High, positive correlation coefficients were found ... between the maximum force of the isometric contraction and the impulse of the MAP."

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ERRATA

2.

- Page 145. CONCLUSION. Second paragraph, last sentence should read "The stimuli which were presented monocularly or as a single change in sound level in these experiments were not effective in significantly altering the response level."
- Page 150. Second paragraph, first word should read "Corticofugal".
- Page 155. DISCUSSION. First paragraph, last sentence should read "Not more ... for any S when both the mechanical and electrical responses were considered together and the significant differences ... varied in sign between Ss."
- Page 170. This should be headed "Table VIII".
- Page 204. Second paragraph, line 5 should read "... control over the reflex ..."
- Page 211. Second paragraph, line 2. Delete the word "on".

a. m. blake

ADDENDUM

Page x. The following publication should be included.

Clarke, A.M. Summation of motor units in a mechanically elicited phasic stretch reflex in normal human subjects.

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a. m. Clarke

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PREFACE

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Clarke, A.M. Specifications and characteristics of a sound-proofed, electrically shielded and thermally insulated room.

Austral. J. Psychol., 1965, 17, 124-132.

The relationship between the electromyogram and the force of the isometric reflex response of normal human subjects.

Nature (Lond.), 1965, 208, 551-552.

The effect of stimulation of certain skin areas on the extensor motoneurons in the phasic reaction of a stretch reflex in normal human subjects.

Electroenceph. clin. Neurophysiol., 1966, 20, 185-193.

Clarke, A.M. The effect of the Jendrassik manoeuvre on a phasic stretch reflex in normal human subjects during experimental control over supra-spinal influences. J. Neurol. Neurosurg. and Psychiat. (in press).

Motoneuron reflex response during intermittent visual stimulation as an indication of fusimotor activity. Physiol. and Behavior (in press).

Relationship between the electromyogram and the isometric reflex response under pre-strain conditions in normal human subjects.

Nature (Lond.) (in press).

LIST OF ABBREVIATIONS

The following abbreviations have been used in this thesis.

| | |
|-----------|-------------------------|
| CNS | Central nervous system |
| E | Experimenter |
| EEG | Electroencephalogram |
| EMG | Electromyogram |
| JM | Jendrassik manoeuvre |
| MAP | Muscle action potential |
| RF | Reticular formation |
| S | Subject |
| S^2 | Variance |
| SD or S | Standard deviation |
| \bar{x} | Mean |

SUMMARY

The spinal pathways for the stretch reflex are quite simple but the response can be modified by supra-spinal activity. Hence, the neural system is a favourable one for investigating some of the ways in which spinal and supra-spinal systems function.

Examination of the neurophysiological evidence dealing with the muscle spindle and stretch reflex permits the following conclusions:

- (a) the stretch reflex is dependent functionally upon the excitation of the primary ending of the muscle spindle,
- (b) the neural pathway involves only one synapse at the spinal cord,
- (c) for small extensions of the muscle the reflex is well localised, occurring only in the muscle subjected to extension,
- (d) the spindle has its own exclusive motor innervation by way of fusimotor neurones which adjust the intrafusal fibres for different initial lengths of parent and extrafusal fibres, and
- (e) the stretch reflex normally is under supra-spinal control especially from the brain-stem RF region.

The impulse of the isometric contraction (that is, the area under the myogram)

The aim of the research was to extend the knowledge of how the human stretch reflex functions. The experiments were psycho-physiological in character; the methods used involved (a) the behavioural control of relevant variables - except in one experiment when an interneuronal blocking agent was used, and (b) the use of natural stimuli with intact, normal Ss.

A phasic stretch reflex (patellar reflex) was investigated by isometric recording because, under this condition, the EMG and force responses are readily quantifiable. Manipulation of both supra-spinal activity and receptor responses was employed.

In order to achieve consistent reflex responses as a base-line for comparison with the various experimental treatments, control was exercised over certain environmental and organismic variables. This was done by conducting the experiments in an environment where stimuli impinging on the S were reduced and by training the S to dampen supra-spinal and muscular activity by applying Jacobson's method of relaxation.

Highly significant, positive product-moment correlations and linear relationships were found between the following pairs of variables:

- (a) the impulse of the MAP (that is, the area between the di- or tri-phasic record and the axis of the EMG) and the impulse of the isometric contraction (that is, the area under the myogram)

- (b) the impulse of the MAP and the maximum force of the isometric contraction (maximum height of the myogram), and
- (c) the impulse of the isometric contraction and the maximum force of the isometric contraction.

A very narrow distribution of the temporal aspects of the myogram (that is, contraction time and response time) was found. The evidence indicated that the responses were likely to be twitches of units or groups of units operating in parallel and adding arithmetically.

When consistent control level responses to uniform taps on the ligament were achieved, a series of experiments was programmed using various stimuli which would affect the S's exteroceptors and interoceptors differentially.

The effect of stimulation of certain ipsilateral skin areas on the reflex was investigated. The reflex was augmented by scratching over rectus femoris but was not affected by similar stimulation over the hamstring or abductor hallucis muscles.

Bilateral presentation of brief trains of auditory and visual stimuli in the form of clicks and light flashes strongly augmented the reflex. Continued presentation of these stimuli resulted in responses which were not dissimilar from control responses. Monocular presentation of brief trains

of light flashes resulted in up to 68 per cent reduction in response compared with binocular stimulation.

Experiments were conducted using a briefly executed contraction of a remote muscle (JM) during (a) normal relaxation of rectus femoris, (b) active contraction of rectus femoris (pre-strain) and (c) intake of an interneuronal blocking agent (Myanesin). The effect of a sustained JM also was investigated. These procedures were used in the expectation that there would be differential effects of descending influences during JM and Myanesin treatments, while the spindles would be unloaded during pre-strain treatment.

Systematic pre-strain treatments ($\frac{1}{2}$, 1 and $1\frac{1}{2}$ kg levels) were used to test the assumption that the spindles would be unloaded and to examine the relationship between the mechanical and electrical responses under these conditions.

Mental activity in the form of calculations in arithmetic, and auditory stimulation in the form of changes in sound level using a 1000 cps tone, failed to have any consistent effect on the reflex.

The general findings were that it was possible differentially to arouse supra-spinal levels of the CNS, presumably the reticular nuclei, with consequent parallel effects of augmentation and attenuation of the patellar reflex. Also, modification of the receptor response was possible by unloading the

spindles during rapid, active contraction of the rectus femoris muscle prior to the tap on the ligament used to elicit the reflex.

Objective, reliable and readily quantifiable indices of fusimotor activity were developed: In all the experiments in which increased fusimotor activity was expected there was an increase in the variance and mean of responses concurrently with a reduction in latency, compared with control responses; when fusimotor activity was assumed to be attenuated, the three indices (variance, mean and latency of the responses) were not dissimilar from control; when the spindles were unloaded during pre-strain so that fusimotor biasing was reduced greatly, the variance was less than control (no valid comparison of the means could be made between pre-strain and control responses because muscle tonus was altered between treatments; no adequate statistics were available for latency observations because the timing apparatus was not designed to function during pre-strain conditions).

The linearity of the relationship and the size of the correlation coefficient between the mechanical and electrical aspects of the response were not affected by supra-spinal influences. However, if observations over a range of muscle tonus were amalgamated for the purpose of calculating a correlation coefficient, a reduction in the size of the coefficient (sometimes significant) was observed.

The general results of the programme of research indicate that under conditions of careful control with intact, normal human Ss, it is possible to modify the reflex responses either by central mediation from supra-spinal levels or by peripheral manipulation of the spindle receptors. These modifications resulted in predictable changes in the measures of the patellar reflex which indicated that the gamma-spindle system is a sensitive indicator of reticular activation.

Half a century so that there is fairly extensive knowledge of the characteristics of this spinal reflex.

The basic spinal circuit is monosynaptic and comparatively simple but a most favourable feature, from an experimental viewpoint with intact humans, is the modification of the stretch reflex which takes place from supra-spinal levels of the CNS. The interaction between spinal and supra-spinal levels of the nervous system provides for the experimental study of the reflex in order to gain information about some aspects of the functioning of both systems. In other words, the study involves the psycho-physiology of the stretch reflex.

Reasons for the research

The greater part of the research on the physiology of the muscle spindle and the stretch reflex has been conducted with infra-human animals, either spinal, decerebrate, anaesthetized or immobilized. The results of that research cannot be extrapolated directly to

CHAPTER I

INTRODUCTION

Why the stretch reflex was selected for study

Experimental neurophysiologists have studied the behaviour of muscle spindles and the neural pathways involved in the stretch (or myotatic) reflex for over half a century so that there is fairly extensive knowledge of the characteristics of this spinal reflex.

The basic spinal circuit is monosynaptic and comparatively simple but a most favourable feature, from an experimental viewpoint with intact humans, is the modification of the stretch reflex which takes place from supra-spinal levels of the CNS. The interaction between spinal and supra-spinal levels of the nervous system provides for the experimental study of the reflex in order to gain information about some aspects of the functioning of both systems. In other words, the study involves the psycho-physiology of the stretch reflex.

Reasons for the research

The greater part of the research on the physiology of the muscle spindle and the stretch reflex has been conducted with infra-human animals, either spinal, decerebrate, anaesthetised or immobilised. The results of that research cannot be extrapolated directly to

human physiology without being tested experimentally in that setting. Nevertheless, the findings have been of vital importance in providing answers to basic questions without which clinicians would be at a disadvantage.

Most investigations on the human stretch reflex have been conducted using unnatural methods of controlling variables. For example, electrical stimulation of afferent nerves is used to assess the contribution of fusimotor biasing on the spindle or procaine is injected into the muscle to block fusimotor fibres selectively.

Obviously, there are limitations to the findings of experiments with animal preparations and to experiments with artificial methods of control in humans. The nervous system of animals has been altered surgically in many cases and in humans, electrical stimuli at best can give an approximate simulation of physiologically evoked nerve discharges.

For these reasons, natural stimuli and behavioural control of relevant variables in a normal, intact human subject would appear to give advantages in extending the knowledge of how the stretch reflex functions in man.

This can be done by gaining a high degree of control over the response so that a base-line can be achieved against which experimental treatments may be evaluated.

Some experimental treatments would include controlled application of different types of natural stimuli. In this way, the CNS at the brain stem level, or above, can be aroused differentially so that the

reflex response is modified in predictable ways. That is, the receptor response may be modified from central regions of the system.

Other experimental treatments would include the modification of the receptor response at the periphery. For example, the spindle lies 'in parallel' with the main muscle and responds when extended, thus it could be unloaded and cease to respond under certain conditions of active contraction of the muscle.

In fact, it will be claimed that sufficient control can be achieved over variables which affect the reflex to permit the development of objective, reliable physiological indices of an aspect of supra-spinal modification of the reflex response, this aspect being fusimotor sensitisation of the spindles.

Research of this kind should lead to a better understanding of the stretch reflex which serves an important function in the maintenance of muscle tonus and postural reflexes. The results of the investigation of this area of the nervous system, therefore, hold considerable theoretical and empirical interest.

Figure 1

Schematic representation of the alpha and gamma systems involved in the innervation of mammalian skeletal muscles. Adapted from Hammond et al. (1956, p.234), Peillard (1957, p.236) and Barber (1962, p.238).

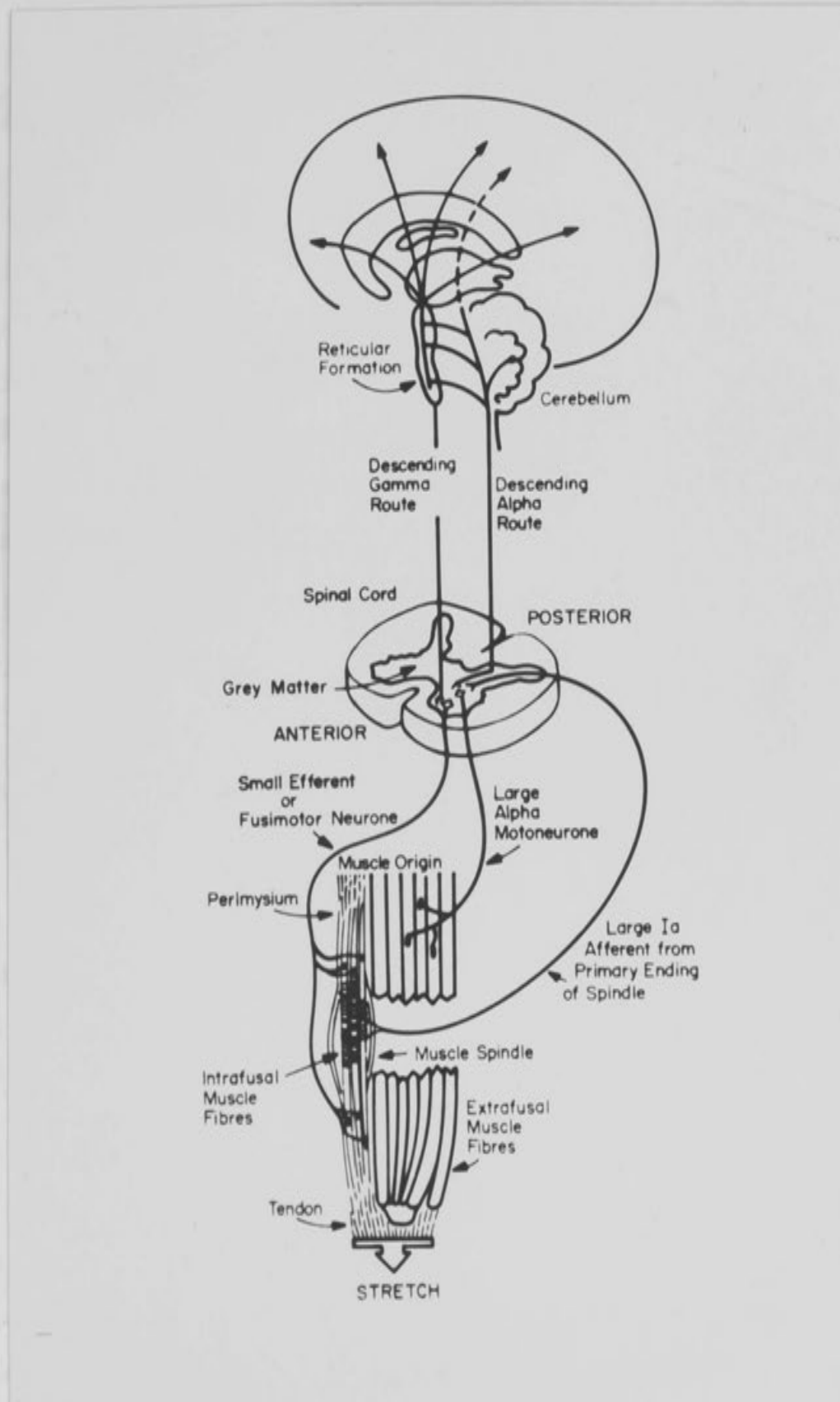


Figure 1

Schematic representation of the alpha and gamma systems involved in the innervation of mammalian skeletal muscle. Adapted from Hammond et al. (1956, p.214), Paillard (1959, p.246) and Barker (1962, p.238).

CHAPTER II

THE NEUROPHYSIOLOGY OF THE STRETCH REFLEX

At this point it would seem appropriate to explain in detail the neurophysiology of the stretch reflex and to give reasons for deciding to investigate the phasic aspect by isometric recording of the patellar 'tendon jerk'. Figure 1 illustrates diagrammatically and in a simplified way, the neural pathways involved in the stretch reflex.

It is proposed to examine the evidence which permits the conclusions that:

- (a) the stretch reflex is functionally dependent upon the excitation of the primary afferents of the muscle spindles.
- (b) The neural pathway is relatively simple there being only one synapse in the spinal cord in the lumbar region in the case of the patellar reflex.
- (c) For small extensions of the muscle the reflex is well localised occurring only in the muscle subjected to stretch. Synergist and antagonist muscles are inhibited or unaffected under these conditions.
- (d) The spindle has its own exclusive motor innervation by way of gamma efferent (fusimotor) neurones which adjust ('bias') the intrafusal

fibres of the receptor for different initial lengths of parent extrafusal fibres. This results in an efficient response to various rates and amounts of extension of the muscle.

- (e) Alpha motoneurone response may be affected by two modes of central influence:
- (i) the indirect fusimotor pathway which has polysynaptic connections with the brain stem reticular formation, and
 - (ii) the direct alpha pathway which can potentiate alpha ventral horn cells to change the general synaptic impingement on the large motoneurones, so that the sensitivity of the stretch reflex is modified by activity emanating from supra-spinal regions of the CNS.
- (f) In the phasic stretch reflex the brief extension of the muscle results in a synchronous volley of impulses which pass along the afferent and efferent neurones to cause muscle contraction. Under these circumstances, the MAP is a discrete di- or tri-phasic spike.
- (g) There is little change in the length of the muscle during an isometric contraction, compared with considerable shortening in an isotonic contraction, and therefore it is likely that changes in the recorded MAP will be related to the increase in muscle tension.

Sensory receptors in muscle and tendon

There are a number of sensory receptors embedded in muscle and tendon which transmit information to the CNS when a muscle is actively contracted or passively stretched. These receptors are the free nerve endings, Pacinian corpuscles, Golgi tendon organs and muscle spindles. The important consideration is which one of these sense organs initiates the stretch reflex?

Free nerve endings which are distributed widely throughout muscles, tendons, ligaments and joints, are considered to be pain receptors (Fulton, 1955). The laminated, onion-like Pacinian corpuscles, from which afferents conduct relatively slowly by way of small diameter (Group III, 1-4 μ diameter) fibres to the CNS, are thought to signal movement of joints (Gray and Matthews, 1951; Wenger, Jones and Jones, 1956) and deep pressure, either from without (Sheehan, 1933) or when muscles are contracted or stretched (Fulton, 1955).

Golgi tendon organs lie within tendons and muscles and hence cannot signal differences between active and passive extension of the muscle. Afferent fibres from tendon organs (Ib fibres) are large, fast conducting fibres (Group I, 12-20 μ diameter, which transmit impulses at velocities above 70 m/sec) but the receptor has a very high threshold to external stretch (Bradley and Eccles, 1953; Hunt and Perl, 1960) and a low frequency of discharge which suggests that tendon organs initiate autogenetic inhibition to protect the muscle from damage at high tensions (Granit, 1950; Gellhorn, 1953). Their function in inhibiting

contractile responses has been demonstrated in infra-human animals (McCouch, Deering and Stewart, 1950) and in conscious man (Libet, Feinstein and Wright, 1959).

The remaining receptor, the muscle spindle, has two morphologically and functionally distinct sensory endings; the primary, annulo-spiral or nuclear bag and the secondary, flower-spray or myotube. There is general agreement that the stretch reflex is functionally dependent upon the excitation of the primary afferent from the muscle spindle and the relevant evidence to support this conclusion will be reviewed.

The muscle spindle consists of a tiny fusiform, lymph-filled envelope which is attached at its polar regions to the extrafusal fibres so that it is positioned 'in parallel' with the large muscle fibres. Hence, active contraction of the muscle relieves or 'unloads' the muscle spindle of its longitudinal stretch whilst passive extension of the muscle extends the spindle. Hence, unlike the Golgi tendon organ, the muscle spindle responds differentially to these two forms of muscle behaviour (Eccles, 1953; Granit, 1955a).

The capsule of the spindle contains a bundle of small diameter muscle fibres, striated at their ends and with many nuclei in the central regions. These fibres have been classified histologically into two categories; nuclear chain and nuclear bag (Jansen and Matthews, 1962; Matthews, 1964). Collectively, these are called intrafusal fibres and this term will be

used henceforth because the functional distinction between nuclear bag and nuclear chain fibres is not yet clear. There are about 10 intrafusal fibres within the spindle capsule in man (Tiegs, 1953). The terminals for the afferent fibres from the spindle end on the intrafusal fibres: the primary ending is positioned in the equatorial region of the spindle and branches several times to wrap in a helical fashion (hence the name annulo-spiral ending) around individual intrafusal fibres; the secondary ending consists of diverse filaments spreading along the intrafusal fibres (hence the name flower spray ending) towards the polar ends of the equatorial region (Matthews, 1964). The term 'ending' includes all the terminations of a single afferent fibre, even though they often lie on different intrafusal fibres.

Spindle motor innervation

The physiology of the spindle is complicated by a separate motor innervation of the intrafusal fibres. This exclusive innervation of the spindle is obtained by way of gamma efferents or small ($2-7\mu$) diameter motor fibres which are now commonly known as fusimotor fibres (Hunt and Paintal, 1958) whose cell bodies lie in ventral roots (Rushworth, 1961). Attempts have been made to classify types of fusimotor fibres (on the one hand, γ_1 to nuclear bag fibres and γ_2 to nuclear chain fibres on the basis of diameters and conduction velocities; on the other hand, static and dynamic fibres on the basis of functional differences in the response of the spindle primary ending when fusimotor

fibres were stimulated) but as knowledge of the precise effects of these is lacking (Matthews, 1962, 1964; Brown et al., 1965), the term fusimotor fibre or gamma efferent will be used in the general sense to include both types of gamma fibre. No sympathetic innervation of intrafusal fibres has been found in association with the motor innervation (Hines and Tower, 1928).

The intrafusal fibres have visco-elastic properties and are contractile for most of their length (Barker, 1948; Matthews, 1964). They can be made to contract strongly by high frequency impulses from the fusimotor neurones which innervate them whereas low frequency discharge may allow the intrafusal fibres to relax (Barker, 1948; Matthews, 1964). Contraction of the intrafusal fibres thus can bias or change the transducing characteristics of the spindle endings so that their threshold to stretch is lowered (Hunt, 1952; Buller and Dornhorst, 1957; Eldred and Fujimori, 1958; Buller, 1961). Although there is no direct evidence, it is generally accepted that the contraction of intrafusal fibres activates the sensory endings of the spindle by mechanically extending the equatorial region of the intrafusal fibres on which the endings lie (Matthews, 1964). The response of the muscle spindle therefore is a function of the contraction of the intrafusal fibres and the extension applied to the parent extrafusal fibres. In general terms, it is a measure of the relative lengths of the equatorial portion of the intrafusal fibres and the main extrafusal fibres (Eldred, 1960).

The functional significance of the motor innervation to the spindle, which must be of a major importance in muscle control because about 30 per cent of ventral root fibres are involved (Rushworth, 1960; Granit, 1962), seems to be in dealing with the relationship between the length of the equatorial portion of the spindle and that of the extrafusal fibres surrounding it (Granit, 1962). This mechanism allows the spindle to respond to the increment in length and rate of change of length of the muscle over the physiological range of initial lengths of muscle (Kuffler, Hunt and Quilliam, 1951). This feed-back of information about the state of the muscle is necessary to compensate for fluctuations which would otherwise occur in the quality and quantity of afferent discharge from the spindle for any given increment of extension. For example, when a muscle has a certain resting length, a given amount of extension will increase both the frequency of discharge from the spindle (as a function of the rate of extension) and the number of afferent endings excited (as a function of the amount of extension). However, if the muscle is allowed to take a shorter resting length, the same increment of extension would now produce a smaller response unless the fusimotor impulses had re-adjusted the intrafusal fibres to the new length of the muscle.

In this way the fusimotor system enables a full range of afferent discharge rates for any given initial length of the muscle so that there may be a comparable input to the CNS for various amounts and rates of muscle extension (Livingston, 1959). Such a peripheral

feedback system can provide a powerful degree of CNS regulation of sensory input.

Kuffler and Hunt (1952) have pointed out that fusimotor regulation of afferent spindle discharge by alteration of the length of the equatorial region of the intrafusal fibres appears to be of great importance in the regulation of muscle performance. For example, if the fusimotor neurones were paralysed, no impulses would flow to the intrafusal fibres which would become slack. Consequently the spindle would have a very high threshold to extension of the extrafusal fibres while active contraction of the muscle would unload the spindle immediately because it is situated 'in parallel' with the extrafusal fibres and sensory information would cease to be sent to the CNS. An uninterrupted flow of afferent impulses, despite some mechanical shortening of the muscle, is necessary, especially in the maintenance of posture, to provide the CNS with continuous information about the state of tension of the muscle and to enable reflex regulation of muscle contraction (Kuffler and Hunt, 1952).

In summary, the experimental evidence reviewed indicates that the intrafusal fibres have two types of afferent ending and a motor supply but no sympathetic innervation.

The function of the primary and secondary endings

Of the two types of afferent fibres from the muscle spindle, the primary or annulo-spiral ending (Group Ia fibre, 12-20 μ diameter) has a 4 to 9 times lower

threshold to stretch than the secondary or flower spray ending (Group II fibre, 4-12 μ diameter) (Barker, 1948; Hunt and Perl, 1960; Lundberg and Winsbury, 1960; Granit, 1962). Because of the differences in fibre diameter, the impulses along Ia fibres are faster conducting than those along Group II fibres so that impulses from the primary ending reach the CNS more quickly than those from the secondary ending. In addition, there is a difference in the response of the primary and secondary endings to mechanically evoked stretch; the primary ending is much more sensitive to the dynamic component of the stimulus than the secondary ending which responds well to the static state of the muscle but which has an insignificant phasic component (Granit, 1962; Matthews, 1964). It seems probable that the primary endings (whatever the state of the muscle and animal) always show a greater sensitivity to changes in the velocity of muscle extension than the secondary endings which have a slower, more regular discharge particularly related to the total extension of the muscle (Cooper, 1961).

Cooper (1962) has remarked on the striking way in which primary endings of muscle spindles in mammals respond to any form of extension of the muscle when fusimotor innervation is intact and she has suggested that the response 'may be still more perfect when all paths for spindle reflex areas are functioning' as would be the case in normal man.

Experimental evidence explicitly implicating the primary ending of the muscle spindle in the initiation

of the stretch reflex is available in the literature. Lloyd (1943a) was able to demonstrate that large Group I fibres provide the afferent limb for the myotatic reflex and McIntyre (1951) in conclusively confirming these findings, concluded that the primary endings were the particular receptors involved because of the large diameter of the afferent fibres from the ending. Bradley and Eccles (1953) and Granit (1950) using anaesthetised cats, reached the conclusion that the primary endings were entirely responsible for the stretch reflex; no trace of concurrent excitatory action being found in the Ib (Golgi tendon organ) fibres. Magladery and co-workers (Magladery et al., 1951) in a remarkable experiment with normal man using electrical stimulation of peripheral nerves and recording from spinal roots with needles placed within the epidural space, were able to show that Group I fibres were activated in the initial phase of a stretch reflex.

Cooper (1960), Hunt and Perl (1960) and Matthews (1964) in reviewing the literature have concluded that, in general, discharges from primary endings of muscle spindles initiate the stretch reflex. Also, there is substantial agreement (Bradley and Eccles, 1953; Lloyd, 1946; Creed et al., 1932; Hunt and Perl, 1960) that the activation of Group Ia afferent produces inhibition of motoneurons of antagonist muscles (reciprocal innervation). This feature provides a favourable situation, in that the extensor response in the stretch reflex is unlikely to be modified by flexor activity in antagonist muscles.

Having established a case for the functional dependence of the stretch reflex on the excitation of the primary ending of the muscle spindle, it is now proposed to examine the characteristics of the reflex arc involved in this response.

The stretch reflex

Liddell and Sherrington (1925) were the first researchers clearly to define the stretch reflex arc and to recognize its restricted nature from and to the same muscle. The neural pathway for the reflex is comparatively simple; stretch of the muscle excites the primary ending of the muscle spindle and impulses are discharged along the Group Ia afferent fibre at a high conduction velocity, probably in excess of 70 m/sec in man (Cooper, 1961; Matthews, 1964) to monosynaptically excite large diameter alpha motoneurons. Impulses pass down the axons of these cells to excite extrafusal muscle contraction.

It appears to be generally agreed that the neural linkage at the spinal cord is monosynaptic. Carefully controlled experiments with infra-human animals have demonstrated two-neuron-arc discharge involving Group I afferents, using electrical (Lloyd, 1943a) and mechanical (Lloyd, 1943b) stimuli. Further, stimulation of afferent fibres evoked discharges only in the motoneurons of the particular muscle, that is, the characteristics of the stretch reflex were present. Later, Szentagothai (1948) using a degeneration technique and McIntyre (1951) using deafferentation,

both worked on the trigeminal nerve system of cats in such a way that it was possible to dissociate, functionally, the afferent fibres from tendon organs and muscle spindles, and came to the conclusion the primary endings initiate the monosynaptic reflex. These findings were confirmed by Bradley and Eccles (1953) who stated that 'the Ia component appears to be entirely responsible for monosynaptic reflex responses'.

In addition to these studies with lower mammals, two outstanding experiments (mentioned above) have been conducted with intact man using long steel needles inserted within the spinal theca to record reflex activity (Magladery et al., 1951; Magladery, et al., 1952). Despite the limitations of working with normal human subjects, for example, the difficulty of controlling the spread of the electrical stimulus in spinal cells, there was sufficient evidence to make it clear that tendon jerks are subserved, for the most part, by monosynaptic neural pathways.

Localisation of the reflex

It seems reasonably certain that impulses from Ia afferents result in monosynaptic excitation of the motoneurones supplying the same and synergist muscles with concurrent inhibition of antagonist muscles (Hunt and Perl, 1960; Matthews, 1964). This favourable experimental situation seems to hold provided small extensions of the muscle are used, under which circumstances the reflex displays a highly restricted field of action to the muscle subjected to stretch

(Liddell and Sherrington, 1924; Fulton, 1955; Cohen, 1953).

Supra-spinal control of the reflex

Alteration of the threshold of spindle sensitivity by fusimotor influence already has been mentioned. An increase in fusimotor discharge lowers the spindle threshold and results in a greater number of afferent neurones discharging and, usually, in an increase in the frequency of discharge, the result being that more motor units respond (Hunt, 1952; Homma, et al., 1962). This indirect influence on alpha motoneurone response by way of fusimotor neurones probably originates through polysynaptic connections between these neurones and the brain stem reticular formation (Granit and Holmgren, 1955; Hunt and Paintal, 1958), a structure from which spindles may be influenced easily from ipsilateral and contralateral sides (Eldred and Fujimori, 1958). In fact, Granit and Kaada (1953) demonstrated that muscle spindles could be controlled quite accurately (for example, 'driven' faster or slower, or stopped) by stimulation of facilitatory or inhibitory regions of the brain stem which activated fusimotor fibres. Much less precise control was achieved by stimulation of the motor cortex, the anterior lobe of the cerebellum and amygdala (Granit and Kaada, 1953). These findings regarding the brain stem control of the muscle spindle response by way of the gamma efferent pathways have been confirmed and clarified (Granit, 1955b; Hongo et al., 1962; Shimazu et al., 1962; Yanagisawa, et al., 1963). Most brain areas related to

motor performance may affect muscle spindle response but almost the whole of the reticular formation from medulla to the thalamus is particularly effective and can exhibit strong centrifugal control over spindle sensitivity (Eldred and Fujimori, 1958).

More recent work (Appelberg and Emonet-Denand, 1965) has shown that both the static and dynamic sensitivities of the muscle spindle primary endings can be selectively controlled from the ipsilateral mesencephalic region of the brain stem. This finding suggests that a rapidly conducting pathway would be required from the reticular formation to the spindles if control were to be achieved in voluntary phasic movements. Granit and associates (Granit and Holmgren, 1955; Granit, et al., 1959) have reported that a fast process of spindle activation by fusimotor neurones does exist, which they suggest has the task of providing for voluntary phasic action.

However, in the case of the tendon jerk, even this fast descending pathway could not operate to provide continuous fusimotor adjustment of the intrafusal fibres simultaneously with muscle contraction (Granit, 1957). This view is supported by the work of Merton (1951) whose results indicate that the 'silent period' [that is, the pause in the EMG following a tendon jerk elicited by a mechanical tap or following a muscle twitch induced by electrical stimulation (Granit, 1955a)] was the result of the spindles being unloaded during contraction, especially if some shortening of the muscle was allowed to occur. This conclusion was

reinforced by Merton's observation (1951) that the duration of the silent period was related to the contraction time of the muscle. The phenomenon of the silent period can be explained by the finding that primary endings of the spindle cease to discharge or slow their rate of firing during muscle contraction, particularly when muscle shortening occurs (Hunt and Kuffler, 1951; Hunt, 1952) so that the alpha motoneurons are similarly affected.

Hence, it appears that the fusimotor system can exert an influence on the tendon jerk response by altering the tension of the intrafusal fibres of the muscle spindle independently of the resting length of the extrafusal fibres (Granit and Henatsch, 1956) prior to the application of the mechanical stimulus but can play no further part in the spindle response once the reflex has been initiated until after the silent period (Creed et al., 1932; Granit and Henatsch, 1956).

An important associated finding is that the reticular stimulation activated the fusimotor neurones and sensitized the spindle without a simultaneous discharge of alpha motoneurons being observed (Granit and Kaada, 1953; Appelberg and Emonet-Denand, 1965). Thus, the spindle may be biased and yet not fire. Apparently, under this condition, the spindle is 'hair-trigger' set for responding to the smallest increment in length caused by muscle stretch.

It has been shown independently by Terzuolo and Terzian, 1953 and by Granit, et al., 1955 that influences descending from supra-spinal levels not only indirectly

affect the alpha motoneurone response by way of alteration in fusimotor sensitization of the spindles but also partly by direct action upon alpha cells in the spinal cord by way of impulses descending in bulbo-spinal tracts (Alpha route, Figure 1). Since the gamma responses to reticular activation have a much lower threshold than the alpha, Livingston (1959) has proposed that

motor facilitation by brain stem mechanisms appears to take place first through an activation of the gamma efferents controlling sensory input from the muscle spindles, and then by both the direct descending influences which act upon the large motoneurons and the continuing indirect influence of brain-stem control over muscle spindle afferent discharges which act back upon the same motor units.

In any event, the gamma and alpha descending routes seem to operate in close association (Eldred and Hagbarth, 1954; Granit, et al., 1959; Granit and Holmgren, 1955) to affect extrafuscal response in infra-human experiments.

The results of all these experiments concerned with the influence of certain regions of the brain stem on gamma and alpha pathways reveal that the efferent functions of the reticular formation encompass basic aspects of phasic and tonic motor activity (Ward, 1958; French, 1960). This is not surprising as Granit (1955a) has pointed out because muscles are concerned with movement; it is appropriate that they should be 'alerted' from supra-spinal levels of the CNS when the organism is aroused and their activity dampened when the organism

rests. In this regard, Rossi and Zanchetti (1957) have pointed out that since the afferent activity from muscle spindles is dependent upon fusimotor discharge which in turn is controlled by reticular influence, a functional relationship would be expected between reticular systems involved in cortical activity and somatic reflexes. They have suggested the diminution of the patellar reflex in man during sleep which has been observed by many workers (Lombard, 1887; Bowditch and Warren, 1890; Lee and Kleitman, 1923; Tuttle, 1924a). Presumably, the significant reduction in gamma discharge allows the intrafusal fibres to slacken in relation to the extrafusal fibres so that the threshold of the spindle rises greatly and thus small extensions of the muscle fail to excite sufficient receptors to cause an overt reflex response.

Another source of supra-spinal influence on muscle reflex activity is the labyrinth. Sherrington (1906) noted the importance of the labyrinth in reflex control of the tonus of many muscles including extensor muscles of the thigh whilst more recent work by Cohen (1953) seems to be explainable in terms of labyrinthine influence on the stretch reflex. Cohen found that when the animal's head was turned towards the limb there was an increase in the resting tension of the muscle whilst the stretch reflex was inhibited when the head was turned away from the limb. These findings indicate that the labyrinth does play a role in control of tonic reflexes and therefore a standard, symmetrical body, head and limb position should be adopted.

Muscle action potentials in the patellar reflex

An important feature of the patellar reflex is that when the 'fast' or phasic, white coloured rectus femoris is briefly extended by a sudden tap on the ligamentum patellae, the primary endings of the spindles discharge together provided the tonus of the muscle is reasonably uniform throughout its volume. The ensuing volley of afferent impulses preserves its synchrony on the efferent side of the monosynaptic neural circuit (Lloyd, 1943a; Denny-Brown, 1949; Walsh, 1959). Since there are about 20 spindles per gramme of human muscle (Cooper, 1960) a large number of motor units should be induced to discharge resulting in a large discrete MAP which, in a relaxed S is di- or tri-phasic in shape and thus can be quantified readily.

Isometric recording of the response

The isometric method of measuring the reflex response was selected because during the contraction the muscle remains essentially at the same length it had at rest. Strictly isometric (constant length) contractions are not possible because (a) the tendons are elastic enough to allow some shortening of the extrafusal fibres (Granit, 1955; Stacy, et al., 1955; Rodriguez and Oester, 1956) and (b) when the force of the contraction is observed by a transducer coupled to the ankle cuff used to restrain the S's leg, a small movement of the measuring instrument is necessary to measure force (Stacy, et al., 1955). However, with care the amount of change in muscle length may be

kept to very small dimensions. This means that the tension increases during the contraction and falls during the subsequent relaxation. Several reports have appeared in the literature indicating that there is a linear relationship between the tension produced in human muscle by a voluntary isometric contraction and the EMG (Inman et al., 1952; Lippold, 1952; Close et al., 1960). In another study (Ralston et al., 1947) amputees were the Ss. Their muscles had been freed of attachment to bone and being unimpeded by the lever action of the forearm were suited uniquely for the study of muscle action. Cineplastic muscle tunnels were placed through the appropriate muscles and EMGs were recorded during voluntary contraction under isometric conditions. A very close agreement was found between the tension developed at any given length of muscle and the integrated action potential.

In the light of these findings, it would be expected that integrated MAPs for an involuntary contraction recorded isometrically would faithfully reflect the magnitude of muscle contraction.

Conclusion

Because of the various reasons given above, the phasic stretch reflex (patellar reflex) recorded isometrically provides a unique response for experimental investigation. The basic monosynaptic neural circuit occurs at the spinal level but the response of the muscle spindle receptor which initiates the reflex can be modified by activity emanating from

supra-spinal levels of the CNS and this is reflected in the alpha motoneurone response. Therefore, provided control can be achieved over the activity of higher centres in the CNS by reducing environmental or exteroceptive stimuli (a procedure which itself would be conducive to allowing the subject himself to bring interoceptive arousal mechanisms under reasonable control), fairly consistent alpha motoneurone responses should be elicited by a uniform phasic stretch stimulus.

The details of the procedures used to attempt to reduce environmental stimuli impinging upon the S and to train the S to dampen activity in higher centres of the CNS will be given in the next chapter.

When the reflex is elicited by peripheral stimulation of afferent fibres in the nerve supplying the muscle under investigation, the muscle spindle with its associated motor innervation is 'removed' from the neural system and the reflex response may be regarded as an index of the availability of the alpha motoneurone only (Henneman and Galvez, 1951; Angell and Haxby, 1957). A comparison of the results under the two conditions gives an indication of the influence of the reflex.

The various family of anaesthetics, when injected locally, differentially affect the fibres in the mixed nerve, small diameter fibres being blocked in preference to large ones. Matthews and Schubert (1957) developed a technique using dilute procaine whereby the small

CHAPTER III

RATIONALE FOR THE TECHNIQUES USED TO ATTENUATE
FUSIMOTOR DISCHARGE BY NATURAL MEANS

The most commonly used methods of examining the effects of spindle biasing on the phasic stretch reflex are (a) the use of the Hoffmann reflex, (b) the introduction of dilute procaine into the muscle and (c) the absorption of an interneuronal blocking agent.

The mechanically elicited myotatic reflex reflects the degree of excitation of the alpha motoneurones together with the bias of the intrafusal fibres which is brought about by fusimotor excitation. On the other hand, the Hoffmann or H-reflex is elicited by percutaneous stimulation of afferent fibres in the nerve supplying the muscle under investigation. The muscle spindle with its associated motor innervation is 'removed' from the neural system and thus the H-reflex response may be regarded as an index of the excitability of the alpha motoneurones only (Benson and Gedye, 1961; Angel and Hofmann, 1963). A comparison of the results under the two conditions gives an indication of fusimotor influence on the reflex.

The cocaine family of anaesthetics, when injected locally, differentially affect the fibres in the muscle nerve; small diameter fibres being blocked in preference to large ones. Matthews and Rushworth (1957) developed a technique using dilute procaine whereby the small

diameter gamma fibres could be selectively blocked whilst leaving the large alpha fibres unaffected so that afferent discharges from the muscle spindle still could be evoked. This technique has been used to investigate fusimotor function in man. (Rushworth, 1960; Clare and Landau, 1964).

Interneuronal blocking agents of the Mephenesin type are known to reduce polysynaptic transmission whilst leaving monosynaptic pathways unaffected (Berger, 1947, 1949; Henneman et al., 1949; Funderburk et al., 1953; Voorhoeve, 1960). Facilitatory and inhibitory influences descending from all levels of the CNS to the cord are depressed by Mephenesin (Henneman et al., 1949; Domino, 1956) and irregular patellar reflex responses become quite uniform (Berger, 1947). Hence the reflex may be investigated under conditions where supra-spinal impingement on alpha and gamma cells is attenuated.

The initial aim of the present experiments was to achieve a reduction in fusimotor discharge by natural means and therefore the use of Hoffmann reflexes, procaine infiltration and interneuronal blocking agents were not considered at this stage. Myanesin was used, however, as part of the programme in a later experiment.

In the previous chapter it was shown that spindle sensitivity may be affected from supra-spinal centres of the nervous system, particularly the reticular nuclei, which themselves may be activated by exteroceptive stimuli (Livingston, 1959). The rationale for the use of the behavioural techniques to reduce fusimotor

activity, therefore, is based on the assumption that gamma discharge results from the interaction of external stimulation and activation at supra-spinal levels of the CNS. That is, if there is high intensity and variety of exteroceptive stimuli impinging upon the S, supra-spinal levels of the CNS will be aroused and fusimotor discharge will be at a high level. Even when the S is not exposed to a barrage of external stimuli he still may be cognitively alert and unrelaxed. Under these circumstances, one would expect a fair degree of fusimotor discharge. However, when the S is mentally and physically relaxed in a familiar environment where the stimuli impinging upon him are reduced to a minimum, the expectation is that fusimotor activity would be dampened to low levels.

These assumptions are supported by empirical evidence. In animal experiments (von Euler and Soderberg, 1957) it has been found on the one hand that an arousing stimulus desynchronised the EEG and increased muscle spindle activity (which implies fusimotor biasing of intrafusal fibres, provided the muscle does not change in length) whilst, on the other hand, there is a decrease in fusimotor discharge during sleep (Rossi and Zanchetti, 1957). Buchwald and Eldred (1961) also have discussed the likelihood that the gamma system contributes 'to a level of spinal activity compatible with the animal's general level of awareness' such that in an intact alerted animal, a sound stimulus could initiate a higher frequency of fusimotor discharge and so prepare it for movement. At the other extreme of the arousal continuum, Japanese workers (Hongo, et al.,

1962) have observed EEG spindling, which correlates with light sleep, occurring concurrently with decreased activity in the fusimotor neurones. A parallelism between central alertness and the sensitivity of the muscle spindle also has been shown experimentally in man. (Paillard, 1959).

In the light of this evidence, there is reason to believe that there is a high relationship between the level of brain activation and the response of the gamma-spindle system.

The two-fold aim of the present experiments, therefore, was to:

- (a) Arrange an environment in which to conduct the experiments where sensory stimuli impinging on the S were very much reduced in intensity and variety. The requirements regarding the types and intensity of stimuli which must be attenuated may be gleaned from the literature and a survey will be made in this chapter.
- (b) Train the S to dampen supra-spinal and muscular activity by becoming thoroughly adjusted to the test environment and by applying a suitable technique of relaxation. An appropriate method of mental and physical relaxation has been reported in the literature and will be outlined in this chapter.

Environmental variables

Several workers have commented upon the large degree of variance in their results when the patellar reflex is investigated (Bowditch and Warren, 1890; Tuttle, 1924a; Golla and Antonovitch, 1929; Emery, 1944). Tuttle (1924a) was so concerned about the 'ebb and flow' of the responses that he resorted to using the average of eight successive reflexes to attempt to smooth the results, whilst Golla and Antonovitch (1929) admitted that they were astonished by the degree of variability in the individual responses. In each case the report given does not reveal any evidence of special care being taken to eliminate extraneous stimuli. Tentative and minimal efforts were made by Bowditch and Warren (1890) who attempted to remove 'external disturbances' and by Emery (1944) who used a 'quiet room'.

Several other authors have been more explicit in reporting the nature of exteroceptive stimuli which affected their results. Lombard (1887) found that sounds such as voices, sudden noises and some 'forms of music' markedly increased the reflex response particularly if they occurred at the 'moment' the blow was struck. These observations have been confirmed by Jacobson and Carlson (1925) who reported that sounds like voices and noises of passing students or the starting of a car nearby tended to facilitate reflexes.

Both Lombard (1887) and Emery (1925) have demonstrated that the knee-jerk amplitude is negatively related to temperature; low temperature being

associated with heightened reflexes and the converse is also true. Temperature changes of 20°F made within two to five minutes effected marked changes in the height of the reflex. It is well known that muscle responses may be affected by small changes (2°C) in body temperature (Hill, 1956) so that the results obtained in these reflex studies are not surprising. Stephenson (1941) apparently was aware of these effects because the room in which Ss were tested was kept at a fairly uniform temperature, 'so as to maintain a comfortable body heat'. Obviously, the S will be restless if he is not comfortably warm and the reflex responses will be affected by this interaction between environmental and organismic variables. In fact, both Lombard (1887) and Emery (1925) imply in their reports that humidity is an important variable as well as room temperature. Fans were used by Emery and whilst he was able to control for air draughts as a causative factor, evaporation, in association with temperature change, could not be eliminated. In this regard Lombard concluded that the effects of enervating and invigorating weather were different. In that era, no satisfactory devices had been invented to give consistent humidity in a test room.

On the matter of visual stimuli, Bowditch and Warren (1890) showed that a sudden flash of light (from a gas flame in a lantern with a condensing lens to focus the light) generally had a facilitatory effect on the knee-jerk. The powerful effect of photic stimuli on the level of excitation of the cortex is now well known

(Sokolov, 1963) and the level of illumination obviously must be controlled if the reactivity of the reflex pathway is to be consistent.

The effects of noise, temperature and illumination have been examined in investigations by Lundervold (1958). He concluded that 'chilliness, loud noise and bad lighting may have the effect of causing muscles to be contracted more vigorously than normal'.

Lombard (1887) reported that irritation of the skin, such as itching, caused marked reinforcement of the reflex and Cooper (1960), in reviewing the literature dealing with muscle spindles, gave as an example of the low threshold of gamma cells to skin stimulation, the excitatory effect on the knee-jerk in man of handling the limb beforehand. Of course, eliciting the reflex by a tap on the skin over the ligamentum patellae, in addition to firing the primary ending of muscle spindle, would bring forth a shower of fusimotor discharge. These gamma impulses would arrive too late to have an effect on the reflex contraction (as has been shown in Chapter II) but would have a powerful effect on spindle sensitivity for a period following the response. Nevertheless, with proper control over the rate of application of the stimulus (together with training in relaxation by the S), so that sufficient time is allowed for fusimotor discharge to be modified to its original level, satisfactory control should be achieved over the effects of the tap as an arousing stimulus.

In this regard, Golla and Antonovitch (1929) used a regular interval of 6 seconds between stimuli but

they found great variability in the responses. Johnson and Carlson (1928) in using an interval of 8 seconds, were concerned in selecting a period which would cause no fatigue and yet allow the recording of the trend of the knee-jerk during individual hunger contractions. The time interval of 8 seconds probably is the minimum to avoid some carry-over effect occurring because Buller and Dornhorst (1957) reported that, at shorter intervals, the second response is depressed whilst Lee and Kleitman (1923) found that if less than 15 seconds elapsed between taps, the second response sometimes was depressed and sometimes enhanced. The latter workers elicited the knee-jerks at irregular intervals ranging between 15 and 30 seconds and this seems to be a reasonable procedure.

This evidence from the literature indicates that an environment is required for testing in which auditory, visual, tactile and thermal stimuli are brought under control. The essential features would appear to be (a) a comfortable room temperature and humidity, (b) a sound-proofed room to attenuate extraneous noise, (c) a uniform, low-level illumination and (d) apparatus which will not be uncomfortable when in contact with the skin of the S and which will not require adjustment by the E during trials.

The specifications for the apparatus developed to meet these requirements will be given in the next chapter.

Organismic Variables

The provision of an environment in which arousing stimuli are markedly reduced will not be sufficient to ensure an attenuation of supra-spinal influences on the reflex. However, it will provide a situation which is conducive to the dampening of brain activity. The application of a technique of physical and mental relaxation should enable the S to approach a state verging on light sleep and, with practice, to hold this state of reduced arousal at a quite uniform level.

There is ample evidence that intensive cognitive activity is related to the amplitude of the knee-jerk: on the one hand, the reflex is decreased during mental inactivity (Jacobson and Carlson, 1925; Jacobson, 1928) and during light sleep, even disappearing during deep sleep (Lombard, 1887; Bowditch and Warren, 1890; Lee and Kleitman, 1923; Tuttle, 1924a); on the other hand, when the S talks or does mental arithmetical calculations, the knee-jerk often is augmented usually concurrently with increased muscle tonus (Lombard, 1887; Lee and Kleitman, 1923; Tuttle, 1924b; Jacobson and Carlson, 1925; Golla and Antonovitch, 1929; Emery, 1931, 1944; Paillard, 1959). The facilitation of the response seems to be particularly certain if the cerebral activity is emotional in character (Lombard, 1887) as, for example, in the situation where a S is pressed to obtain a result as rapidly as possible and probably the task becomes difficult for him. The fact that an increase in muscle tonus often has been reported in association with an increase in mental effort

indicates the importance of having the S mentally relaxed in order to obtain consistent responses.

Bowditch and Warren (1890) have commented that variations in arousal or 'mental state' were sufficient to cause the large differences they 'observed in successive knee-jerks under apparently identical conditions'. In order to attempt to counter this condition, they resorted to using mentally retarded Ss but, of course, without success because these people are just as prone to fluctuations in arousal as normals.

A general relationship has been found in lower mammals between changing levels of cortical activity detected by electrodes placed on the dura (irrespective of whether the change was experimentally evoked or not) and fusimotor discharge recorded at ventral roots (Buchwald and Eldred, 1961). It would appear therefore that variations which have been observed to occur in muscle tonus during mental effort at least are partly the result of fusimotor biasing of the spindle. The lowered threshold of the receptor may cause some spindles to discharge and elicit a response in alpha motoneurons sufficient to increase slightly the tension in the muscle. Fluctuations in muscle tonus are reflected in the increased variability of the responses. An explanation for the great variability in his results with human Ss has been put forward by Varnum (1934) in terms of the large part played by 'variations in muscle tonus'.

Granit (1950) has observed in animal experiments that muscle tension is an important factor in setting

the excitability level of the motoneurons. The necessity for attempting to gain control over muscle tonus also has been noted by Hagbarth (1964) who in clinical neurophysiology with man has found that 'the most important variable in determining the amplitude of the stretch reflex...is the amount of background activity in the stretched muscle'. Thus it is clear that consistent reflex responses are not likely unless muscle tonus is uniform during trials.

The EMG as an index of muscle tonus

A sensitive indicator of muscle tonus is the EMG. It has the advantage of detecting slight activity in muscle which could be impossible to determine by palpation (Wheatley and Jahnke, 1951) and it is delicate enough to register electrical activity which does not result in a mechanical response (Hines and Knowlton, 1952). When a limb is supported, the S can be trained to relax the muscle so that it is flaccid and contractile activity is absent (Denny-Brown, 1949). Under these circumstances no action potentials can be detected either from surface electrodes on the skin or from needle electrodes inserted into the muscle adjacent to a motor unit (Bauwens, 1948; Hoefer, 1941). The appearance of MAPs is clear evidence of increased activity in the motor units of the muscle underlying the skin electrodes (Newman, 1953). The integrated MAP bears a linear relationship to tension exerted during voluntary isometric contraction and if the same relationship was found to hold for reflex isometric contraction, then the EMG would be a valid index of

muscle tonus. It was decided, therefore, in the present experiments to begin trials only when the muscles under investigation were electrically quiescent; any change in muscle tonus then may be detected as measurable MAPs.

The use of the EMG is indicated also by the evidence that there is a functional relationship between the voltage of the EMG and level of relaxation. In an elegant experiment, Newman (1953) attached electrodes on the skin over the temporal muscle so that when the Ss were relaxed only an EEG was recorded but when they were aroused by 'stimulating' words (prepared from a modified Jung list containing emotional and neutral words in random order) an EMG was super-imposed on the tracing, the muscle action spike standing out clearly from the lower amplitude rhythm of cortical activity. The Ss were seated comfortably in a noise-attenuated, warm environment. The EEG during the relaxed wakefulness was optimal alpha rhythm (in the range 8-13 cps) with no EMG contamination but when the S was aroused by an emotionally toned stimulus, such as a spider 'crawling' onto her arm, the alpha waves were blocked and a burst of MAPs of large amplitude (up to 1.5 mV) and high frequency (up to 60 cps) was observed. This relationship between the EMG and arousal (as indicated by alpha EEG patterns) also has been demonstrated by Bartoshuk (1959) who found that the magnitude of the EMG response was related to EEG activation elicited by a 0.2 sec duration burst of 'white noise'.

The EMG therefore may be used as a sensitive indicator of muscle activity and the S's general state of arousal. The absence of electrical activity in a relaxed and supported muscle need not imply the absence of fusimotor barrage because the potentials at gamma motor end-plates on intrafusal fibres cannot be detected by the EMG (McIntyre, 1965).

Although tonic fusimotor activity or 'background discharge' can occur in intact animals when the alpha motoneurons of the same muscle are not discharging (Matthews, 1964), this does not mean that fusimotor neurones discharge repetitively in the absence of an inflow of sensory impulses. Background activity in gamma pathways is abolished under these circumstances (Hunt and Paintal, 1958) and, in experiments with man, it is likely to be minimal when supra-spinal influences are attenuated to a great extent by the procedure of placing the S in an environment where arousing stimuli are controlled and by training the S to relax mentally and physically. This procedure would seem to be the most promising natural method of gaining a large measure of control over fusimotor function in the intact human where it is not possible or desirable to eliminate gamma activity completely.

Direct recording of intrafusal fibre responses is achieved with great technical difficulty in experimental animals and, of course, it is not possible with intact human Ss. Even in animal experiments, fusimotor discharge generally is inferred from changes in frequency recorded from afferent fibres emanating

from the muscle spindle, provided the tension in the muscle does not alter (Hunt and Paintal, 1958; Eldred and Fujimori, 1958). This procedure thus sets a precedent for using a similar index of fusimotor activity in experiments with man. Instead of recording the frequency of afferent discharge directly with electrodes on the nerve fibre, surface electrodes were used in the present experiments to record the MAP; the assumption being that the motor response will be proportional to the afferent discharge, that is, the MAP should mirror the spindle output. In the case of a phasic stretch reflex, this reproduction should be of high fidelity because the synchrony of the afferent volley of impulses is preserved on the efferent limb of the myotatic arc (Walsh, 1959). Alterations in the response of the spindles to a uniform rate and amount of extension over trials should be reflected in the motor unit responses and, consequently, in the MAP. When muscle length and tonus remain the same, such changes may be attributed to alterations in the threshold of the spindles as a result of fusimotor biasing of the intrafusal fibres. Fluctuations in the sensitivity of the spindles would result in changes in the number of spindles responding and probably in the frequency of firing. These characteristics of the afferent input would be observed as changes in amplitude and variance of the MAP over a set of observations and these measures may be taken as an indirect index of fusimotor bias. The technique is applicable to making decisions about sample sets of observations rather than making the individual

comparisons which are possible in animal studies with direct recording from spindle afferents.

Jacobson's technique of relaxation

The case for the need to dampen supra-spinal activity and to physically relax the musculature of the body and limbs has been presented. It remains to outline the method by which this can be done. The technique of relaxation developed by Jacobson (1924, 1928, 1938) was selected because it appears to meet the requirements.

The general feature of Jacobson's technique is to train the S to recognize tension and relax it. In the present experiments, the S was required to sit in a comfortable chair and, hence, Jacobson's technique for 'differential' relaxation was applied. The S's eyes were covered by a mask and training took place in a sound-proofed, air-conditioned room with the E present. There was a preliminary familiarisation period of one or two hours during which the S became used to the new environment and at ease in the presence of the E. Following this period the S was connected to the apparatus so that he or she could become used to wearing electrodes and having the patellar ligament tapped while the ankle was restrained by a cuff. The EMG was displayed on a fluorescent tuning indicator tube inside the room so that the E could inform the S of the state of electrical activity in the quadriceps and hamstring muscles. The criterion was electrical

quiescence in both muscle groups, that is, equal tone in the agonists and antagonists before the extensor stretch reflex.

Initially, the S was taught to recognize and relax gross tension in these large muscles. Once control was achieved over large muscles, the S was trained to recognize slight tension in progressively smaller muscles. In addition, the S was trained to realise that muscle relaxation is the antithesis of contraction and involves no positive mental effort. Advanced training in relaxation involved (a) extreme muscular relaxation where the S was requested to stiffen a finger without moving it and then to relax it progressively past the stage where it seemed perfectly relaxed, and (b) reduction of mental activity by extreme relaxation of tension in the ocular and throat muscles, such tension being associated with visual and speech imagery (Jacobson, 1924).

By a combination of training in mental and physical relaxation and adjustment to a stimulus-attenuated environment, it was anticipated that the S's level of arousal could be reduced considerably. Under these conditions, there is evidence that supra-spinal influences on the stretch reflex by way of direct and indirect pathways would be attenuated so that a reasonably consistent response should be elicited for uniform stretch stimuli.

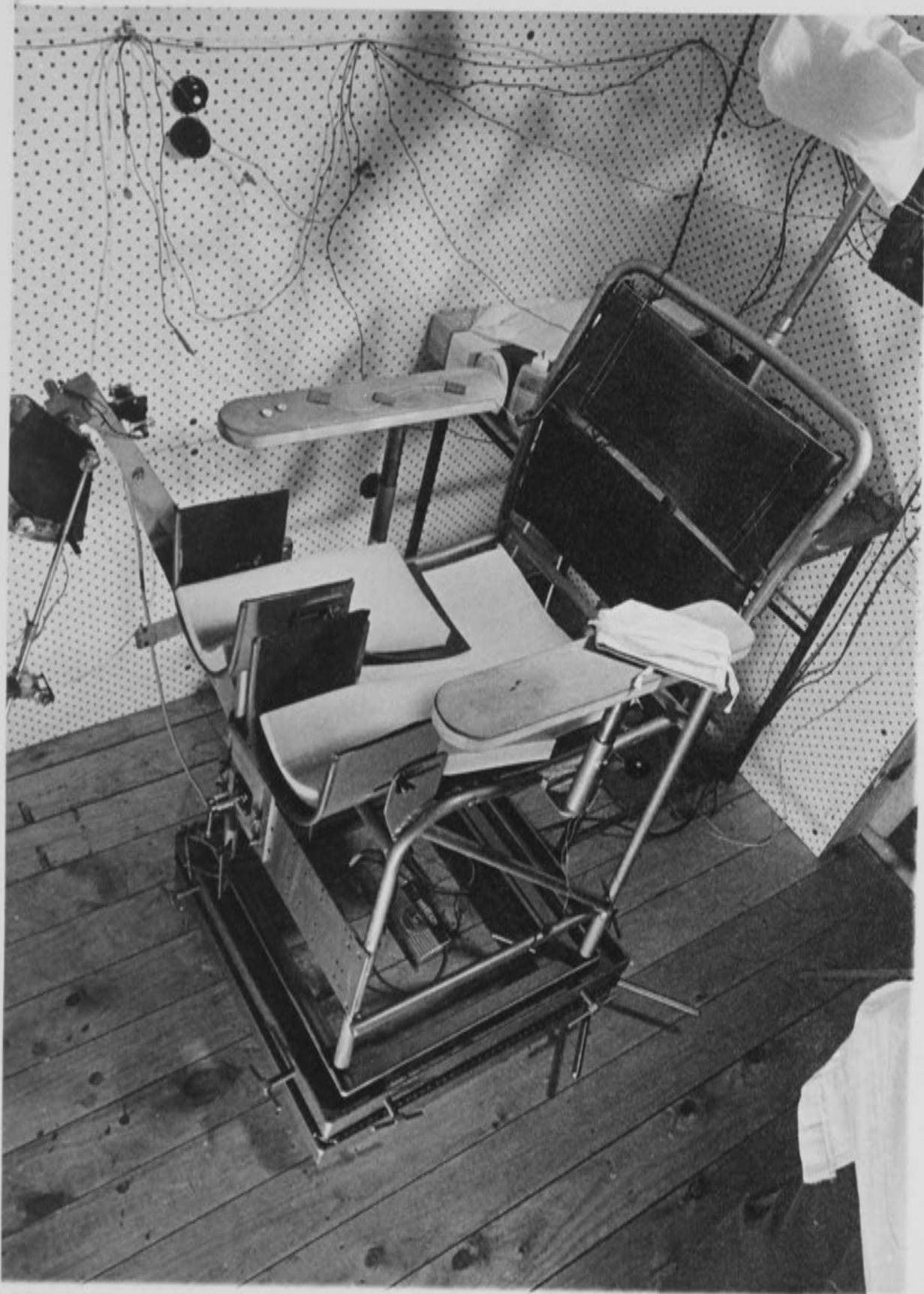


Figure 2

Photograph of the inside of the room showing the chair, pendulum-hammer, ankle-cuff and transducer cell, ground strap and EMG electrodes (right arm of chair), and eye mask (left arm of chair).

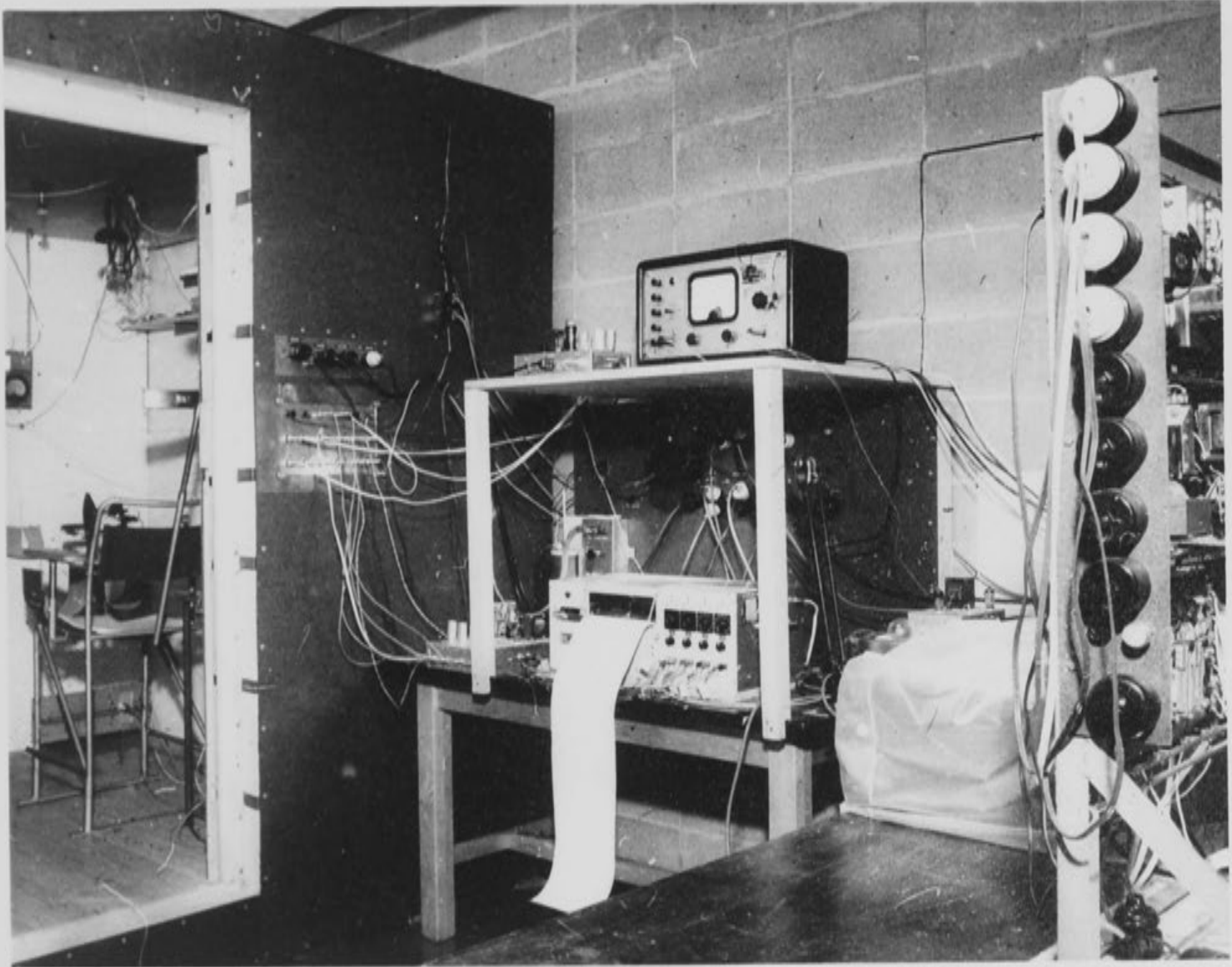


Figure 3

Photograph showing part of the inside of the room and the recording apparatus outside. The meter (for pre-strain experiments), the headphones (for auditory experiments) and the chair can be seen inside the room. The EMG pre-amplifier and Both pen recorder are on the bench with the Chronotron and timing trigger above. Automatic control apparatus is shown on the right.

CHAPTER IV

THE APPARATUS

The principal items of apparatus used in the experiments are described below. Photographs (Figures 2 and 3) show the apparatus and the general relationship between the items.

With the exception of the Both recorder, E.I.L. Chronotron and Statham transducer - load cell assembly, the items of equipment were designed and constructed especially for the experiments.

The details of the apparatus are given below.

1. SOUND-PROOFED, ELECTRICALLY SHIELDED AND THERMALLY INSULATED ('SPESTI') ROOM

This room gave accurate control over

- (i) temperature and humidity
- (ii) noise and illumination
- (iii) interference signals from adjacent electrical equipment outside the room operated by 50 CPS supply.

Tests to determine the characteristics of the room gave the following results.

Temperature and relative humidity

Tests using the air conditioner demonstrated that the unit can heat the room to a maximum of 28°C in

Winter and 32.4°C in Summer, or cooled to a minimum of 17.5°C in Winter and 18.4°C in Summer. For these extremes of temperature, at least three hours were required to achieve stability from ambient room temperature (mean 20.2°C , range 19°C). With the circulation of temperate conditioned air, a high degree of consistency of temperature and humidity can be obtained after one hour. For example, in test periods during Winter reliable control of temperature (mean 19.7°C , SD 0.24°C) and humidity (mean 49.3 per cent, SD 1.5 per cent) was obtained over six hours following the initial one hour settling period.

Table A shows comparative data for dry bulb temperature and relative humidity taken simultaneously inside and outside the Spesti room under conditions of cold, temperate and hot room climate. These records were obtained without the observer present in the room but additional tests showed that the effect of having a person in the room was to raise dry bulb temperature by 1.4°C and relative humidity by 5 per cent.

A smoke taper test revealed that no pronounced air currents occurred in the room, even when the air conditioner was operated at maximum air delivery speed of $230\text{ ft.}^3/\text{minute}$. The outlet duct cleared the room of smoke in thirty minutes using the maximum ventilation rate of $120\text{ ft.}^3/\text{minute}$.

TABLE A

Simultaneous Observations Taken Inside and Outside
the Room of Dry Bulb Temperature
and Relative Humidity Under Three Climatic Conditions

| | | Room Climate | | | |
|-------------------------|----|------------------|----------------------|----------------|-----------|
| | | Cold 10 hours | Temperate 9 hours | Hot 6 hours | |
| INSIDE SPESTI ROOM | | | | | |
| Dry bulb temperature | °C | Mean | 18.8 | 22.1 | 31.6 |
| | | Range | 18.4-19.2 | 22.0-22.4 | 31.0-32.4 |
| Relative humidity | % | Mean | 58 | 43 | 40.5 |
| | | Range | 54-61 | 41-44 | 40-41 |
| OUTSIDE SPESTI ROOM | | | | | |
| Dry bulb temperature | °C | Mean | 21.5 | 21.3 | 22 |
| | | Range | 21.0-22.5 | 21.0-22.0 | 21.0-23.2 |
| Relative humidity | % | Mean | 58 | 56 | 52 |
| | | Range | 55-56 | 48-63 | 40-63 |

Note - Data recorded with room empty.

Sound attenuation

Instrumental techniques can only approximate the subjective appreciation of sound intensity for binaural listening (Broch, 1962; Stacy, et al., 1955). However, adequate estimations of the effectiveness of the Spesti room design can be obtained with sound level meters (American Standards Association, 1961; Beranek, 1954). Measurements were made of the attenuation of (a) sound pressure level using the linear scale of a Bruel & Kjaer

(Type 2203) instrument and (b) sound level using the weighting networks of a Dawe (Type 1400E) instrument, the A, B and C scales of which approximately correspond to the 40, 70 and 100 phon equal loudness level contours, respectively, of Robinson & Dadson (1956).

The Dawe instrument was used to measure sound level so that direct comparisons could be made with the attenuation characteristics of the Canterbury room (Rodda, et al., 1963) and the Cambridge room (Thorpe and Hinde, 1956), the readings in those reports being made with Dawe meters.

Ambient sound pressure level outside the Spesti room ranged from 48 to 72 db. (Lin) with a mode of 52 db. (Lin) whilst readings on the weighting network were 34 to 46 db. (A) (range) and 36 db. (A) (mode).

Table B shows the ambient sound pressure levels and ambient sound levels when the room air conditioner is (a) switched off, (b) functioning with low air intake and (c) functioning with high air intake. The appreciable fall in reading when switching from the linear scale to the weighting scale indicates that the ambient sound is characterized mainly by low frequency components and these are very difficult to attenuate.

The modal ambient sound level under condition (b), which is the normal operating state, is 49 db. (C) measured with the Dawe meter. This is less than the mean allowable background noise, in the range 300 to 9600 c.p.s., of 50.4 db. (C) for audiometry rooms suggested by Glorig (1958).

TABLE B

Ambient Sound Pressure Levels and Sound Levels
for Various Conditions Within the Room
With the Observer Present

| Room condition | Sound pressure level; db. (Lin) Bruel and Kjaer, 2203, SLM | | Sound level; db. (Weighted) A Scale, Dawe, 1400E, SLM | |
|-----------------------------------|--|------|---|------|
| | Range | Mode | Range | Mode |
| Air conditioner off | 45-51 | 47 | 32-35 | 33 |
| Air conditioner on low intake | 53-58 | 55 | 34-37 | 35 |
| Air conditioner on high intake | 54-59 | 57 | 36-39 | 37 |

Table C gives comparative data recorded outside and inside the room for various frequencies in the range 0.3 to 6 kc.p.s. with 100 db. (C) Dawe sound level outside the room (except at 300 c.p.s. where 95 db. [C] was the maximum amplification possible with the instruments used). A decrease in the degree of sound attenuation with decrease in frequency applies to the Spesti room for both sound pressure level and sound level, and appears to be a characteristic of the Canterbury and Cambridge rooms, also.

The average sound attenuation of the Spesti room over the frequency range studied was 44 db. (Lin) for sound pressure and 44.3 db. (Weighted) for sound level. This compared with a mean attenuation of 40 db. (frequencies 0.5 to 6 kc.p.s.) between the apparatus room and the inside of the Canterbury sound proof room

TABLE C

Comparative Sound Pressure Levels and Sound Levels for Various Frequencies Measured Inside and Outside the Room^a

| Source fre- quency c.p.s. | Sound pressure level; db. (Lin) ^b | | | | | Sound level; db. (Weighted) ^c | | | | |
|------------------------------------|--|------|--------|------|------------------|--|--------|--------|--------------------|------------------|
| | Outside | | Inside | | Atten- uation | Outside | | Inside | | Atten- uation |
| | Range | Mode | Range | Mode | | Range | Mode | Range | Mode | |
| 6000 | 96-97 | 96 | 45-49 | 47 | 49 | 98-101 | 100(C) | 46-50 | 48(A) ^d | 52 |
| 5000 | 96-98 | 97 | 50-54 | 51 | 46 | 100-101 | 100(C) | 44-49 | 46(A) | 54 |
| 4000 | 93-95 | 94 | 50-52 | 50 | 44 | 100-101 | 100(C) | 54-58 | 55(A) | 45 |
| 2000 | 98-99 | 98 | 55-56 | 55 | 43 | 99-100 | 100(C) | 55-58 | 56(B) | 44 |
| 1000 | 98-100 | 100 | 61-62 | 62 | 38 | 100-101 | 100(C) | 56-59 | 58(B) | 42 |
| 500 | 96-97 | 97 | 53-56 | 56 | 41 | 100-101 | 100(C) | 59-62 | 60(B) | 40 |
| 300 | 98-99 | 98 | 62-63 | 62 | 36 | 95-96 | 95(C) | 61-62 | 62(B) | 33 |

a In all cases, observations were made 6 feet from the source of the test sound, with the air conditioning unit switched off and with the observer present.

b Bruel and Kjaer, 2203, SLM.

c Dawe, 1400E, SLM.

d Indicates the weighting scale used in taking the measurement.

and a mean attenuation of 65 db. for the Cambridge room which was built especially to eliminate frequencies of 2 kc.p.s. and above (Thorpe and Hinde, 1956; Rodda, et al., 1963).

Using the formula $\frac{P}{P_0} = \text{anti log } \frac{\text{db.}}{20}$, a ratio of 158/1 for average pressure attenuation was calculated.

Vibration attenuation

Measurements of the vibratory characteristics of the Spesti room were made with a Bruel and Kjaer sound level meter (Type 2203) by means of an input adaptor and accelerometer (Type 4328) for which a correction factor of 36 db. was applied.

A weight was dropped from a fixed height on to the concrete floor and vibration measurements were taken equidistant from the place of impact, inside and outside the room.

The energy expended (1.5 ft. lbs.) by impact imparted on acceleration of 26 db. re 1 cm/sec² (rms) on the floor outside the room, and the acceleration measured on the floor inside the room was 6 db. re 1 cm/sec² (rms). This reasonably isolated internal state probably resulted from the combined use of the two constructionally separate shells and two sets of rubber mountings.

Electrical attenuation and interference supression

The main concern was the supression of 240V (50 c.p.s.) AC from electrical instruments and cables adjacent to the room. The 50 c.p.s. frequency lies

within the spectrum encountered in electro-physiological variables and may induce noise on the wave form of the bio-electric signals.

A wire loop was made to fit closely in the vertical plane around the outside of the Spesti room and 50 c.p.s. current was fed into the loop via a transformer from the mains supply. The signal emitted was measured with a Philips (Type GM6012) voltmeter with the detector aerial in two positions; (a) inside the room in a position where the largest signal was received and (b) outside the room with the aerial in the same relative position as for condition (a). An attenuation ratio of 250/1 or 48 db. was obtained (Table D).

TABLE D

Comparison of Voltages from Two Signals
Received Inside and Outside
the Shielded Room

| Frequency | Voltage | | Attenuation | |
|------------|---------|-----------|-------------|-----|
| | Outside | Inside | Ratio | db. |
| 44 kc.p.s. | 1.4 mV | 7 μ V | 200/1 | 46 |
| 50 c.p.s. | 0.25 V | 1 mV | 250/1 | 48 |

Although outside the frequency range of electro-physiological measures, a steady signal of 44 kc.p.s. was used as a second means of measuring electrical attenuation. Since the source of the signal was several miles distant, the electro magnetic field was uniform in the area of reception and therefore direct readings were taken inside and outside the room using a

Hewlett-Packard wave analyser (model 302A) with a loop aerial oriented for maximum signal. The attenuation ratio of 200/1 (Table D) was considered satisfactory.

No differences in suppression of electrical interference were found when the earth was disconnected from the bronze mesh shields and/or the input leads were unplugged from the 12V DC 'house system'.

However, when EMG potentials were recorded from surface electrodes inside the room, a further reduction in 50 c.p.s. interference was obtained when the ground wires from the power sockets to the amplifier and pen recorder were disconnected and the instruments grounded by way of the metal braid of the shielded cables from the panel on the wall of the Spesti room. Presumably, current circulating in ground loops resulted in voltages which interfered with the signal and this was prevented by using one ground connection only to each instrument.

2. THE SUBJECT'S CHAIR

The chair was constructed of tubular steel with extra long legs so that the S's feet did not touch the floor. Adjustable head, arm and thigh supports together with a padded seat and back rest enabled individual Ss to be seated comfortably. All parts which were likely to come into contact with the S's skin were covered with non-conducting material (mainly thin felt).

The pendulum-hammer was pivoted from metal bars attached to the frame of the chair whilst the

transducer-load cell unit was secured to a metal frame bolted across the front legs.

3. TRANSDUCER AND LOAD CELL UNIT

A Statham bi-directional, universal transducing cell (Model UC2) to which was attached a load cell accessory (model UL4-20) was bolted to the front plate of the chair. A four-piece, adjustable metal ankle cuff was attached to the load cell with a ball and socket joint in the linkage as a protection against non-axial loads.

Signals representing the force-time relations of the reflex response were pre-amplified through a transistorised DC circuit (Figure 28, Appendix A) before being fed to the DC amplifier of a Both pen recorder.

The transducer-load cell unit was calibrated by suspending it vertically and hanging accurate weights from it.

4. PENDULUM-HAMMER

A pendulum-hammer weighing 220g was released by hand to fall under gravity to tap the ligament and elicit the reflex. The length of the arm could be adjusted for individual Ss (approximately 30 cm). The area of the percussion face was 2.5 cm by 1 cm.

A silicon, P-type, strain gauge (346 ohms resistance) was mounted into the head of the hammer to measure the force-time relations of the tap on the

ligament (Figure 29, Appendix A). Signals from the strain gauge were pre-amplified through a transistorised DC circuit (Figure 30, Appendix A) before being fed to the DC amplifier of a Both pen recorder.

The strain gauge response was calibrated by resting accurate weights on the percussion face of the hammer head whilst it was secured in a vertical position.

5. ELECTRODES, PUSH-PULL AMPLIFIER AND RECORDER FOR EMG SIGNALS

MAPs were received by pairs of hollow disk silver electrodes placed 9.5 cm over the belly of the muscles quadriceps (rectus femoris) and hamstring (biceps femoris).

The skin was prepared by (a) shaving closely with a razor to remove hair and scaly skin and (b) rubbing in electrode jelly. The electrode cups were filled with the conductive jelly.

Electrical potentials were pre-amplified through push-pull circuitry (Figure 31, Appendix A) and fed to the DC amplifier of a Both pen recorder. Calibration was achieved by using an instrument to deliver known voltages at the electrodes (Figure 32, Appendix A).

The paper speed of the pen recorder was 50 mm/sec. In order to conserve paper, the motor drive was operated for 3 sec during each trial during which time the records were made. This was accomplished by suitable relays which E triggered with a hand switch just before each trial began. Electrical artifacts in the record

brought about by starting and stopping the motor drive were eliminated by using the circuit shown in Figure 33, Appendix A.

6. CHRONOTRON AND TRIGGER TO MEASURE LATENCY

Latency (defined as the interval in msec from the instant the pendulum-hammer struck the skin over the ligament until the initiation of the first synchronous MAP in rectus femoris) was measured by the following method.

A miniature micro-switch mounted on the edge of the hammer (Figure 29, Appendix A) closed when the percussion edge struck the skin over the ligament and started the chronotron (Electronics Instruments Ltd., Model 25E). The input to the pen of the channel recording the EMG from rectus femoris in the Both recorder was connected to the trigger circuit (Figure 34, Appendix A) and to the chronotron. When the first synchronous MAP began to rise in voltage the trigger circuit operated to stop the chronotron.

7. AUXILIARY APPARATUS

(i) Visual display of EMG signals

When necessary the EMG signals could be displayed on two fluorescent tuning indicator tubes so that the E could view the level of electrical activity in the muscles. The circuit for this system is shown in Figure 35, Appendix A.

(ii) Sound and visual stimuli

Sound stimuli were presented binaurally through headphones by means of

(a) a frequency oscillator when a tone of 1000 cps was required

or (b) a battery powered, capacitor and resistor circuit when clicks were required (Figure 36, Appendix A).

Light flashes were presented by means of a neon tube and a similar battery powered circuit when required (Figure 36, Appendix A).

- (b) which of the dependent variables yield the most reliable information about the isometric reflex contraction, and
- (c) what relationship exists between the dependent variables because this had not been reported in the literature.

The plan was to control the relevant variables which were likely to affect the myoelectric reflex. If the variance of the response was small then it was proposed to go ahead in later experiments to investigate the effect of different types of stimuli on the reflex. However, if the variance was large, then it was proposed to investigate, systematically, the variables which contribute to the variance. In effect this experiment was a test of the efficiency of the controls which were proposed in Chapter III.

CHAPTER V

THE ASSESSMENT OF CONTROL PROCEDURES
AND THE INVESTIGATION OF RELATIONSHIPS
BETWEEN PHYSIOLOGICAL MEASURES
OF THE PATELLAR REFLEX

The aims of this preliminary experiment with the patellar reflex were to find out:

- (a) what degree of invariance could be attained using the methods of control which had been decided upon
- (b) which of the dependent variables yield the most reliable information about the isometric reflex contraction, and
- (c) what relationship exists between the dependent variables because this had not been reported in the literature.

The plan was to control the relevant variables which were likely to affect the myotatic reflex. If the variance of the responses was small then it was proposed to go ahead in later experiments to investigate the effect of different types of stimuli on the reflex. However, if the variance was large, then it was proposed to investigate, systematically, the variables which contribute to the variance. In effect this experiment was a test of the efficacy of the controls which were proposed in Chapter III.

To recapitulate, the variables to be controlled are listed, briefly, below. They are dichotomised for convenience although precise categorisation is unwarranted because interaction occurs between the two sets of variables.

Environmental variables

Ambient temperature and humidity of the room.
 Noise from outside (pen recorder motor, passing cars) or inside (movement of apparatus or the E speaking) the 'Spesti' room.
 Illumination level.
 Rate of application of the tap on the ligament.
 Placement of the tap on the ligament.

Organismic variables

Mental and muscular relaxation.
 Body and limb position.
 General level of behavioural activity prior to testing.
 Time of eating in relation to test session.
 Extension of the muscle by deflecting the ligament.

The methods used to prepare a S for a test session were as follows:

Four males and three females participated and were asked to maintain a consistent, moderate level of behavioural activity over the whole period of the experiments. Where a very late night or strenuous physical exercise could not be avoided, the experimental session following was abandoned because consistent

responses were found to be impossible under these circumstances.

The time of day for testing was held constant for each S because diurnal variations exist in the patellar reflex (Lombard, 1887). This condition also indirectly controlled time of testing in relation to food intake, a necessary precaution because during hunger periods there is an augmentation of the reflex (Johnson and Carlson, 1928).

The Ss had been trained in Jacobson's method of mental and physical relaxation for at least six separate one hour sessions spread over two weeks before this experiment began.

The experiments were conducted in the 'Spesti' room. Ambient dry bulb temperature was held at $25^{\circ}\text{C} \pm 2^{\circ}\text{C}$ and relative humidity at 50 per cent ± 6 per cent over the period of all the experimental sessions. Extraneous noise from outside the room was attenuated at least 44db and the E conducted operations silently within the room. The S's eyes were covered with a cloth mask tied behind the head and as a precaution, the illumination within the room was reduced to 21.5 lumens/sq metre (that is, just sufficient to allow the experimenter to see the writing on his protocol).

The head, arm and thigh supports of the chair as well as the ankle cuff were adjusted for each S so that a comfortable, upright and symmetrical body and limb position was achieved.

The length of the pendulum was adjusted to that the hammer struck the ligamentum patellae mid-way between the apex of the patellar and the tubercle of the tibia. The force of the tap was adjusted at the beginning of each session so that it was just over the threshold necessary to elicit a brisk reflex. The trials were conducted at irregular intervals of not less than 15 seconds.

The arm of the pendulum-hammer was held against a plastic covered stop by the experimenter before being released and caught by hand on the rebound so that the whole operation was executed silently.

Electrode positions on quadriceps and hamstring muscles were standardised for individual Ss, the distance between electrodes being 9.5 cm. These places were marked with gentian violet antiseptic and re-touched when necessary.

Figure 4 shows the general experimental arrangement of the EMG electrodes, ground strap, pendulum-hammer and transducer load-cell.

Testing was not begun unless the following criteria were achieved for the EMG. In rectus femoris, quiescence before and immediately following the tap on the ligament, and discrete di- or tri-phasic MAPs (indicating highly synchronous motor unit discharge) in response to the brief stretch of the muscle. Hamstring activity was expected to be negligible, that is, less than $25\mu\text{V}$ at any time. Figure 5 shows the response of a trained S which meets the criteria.

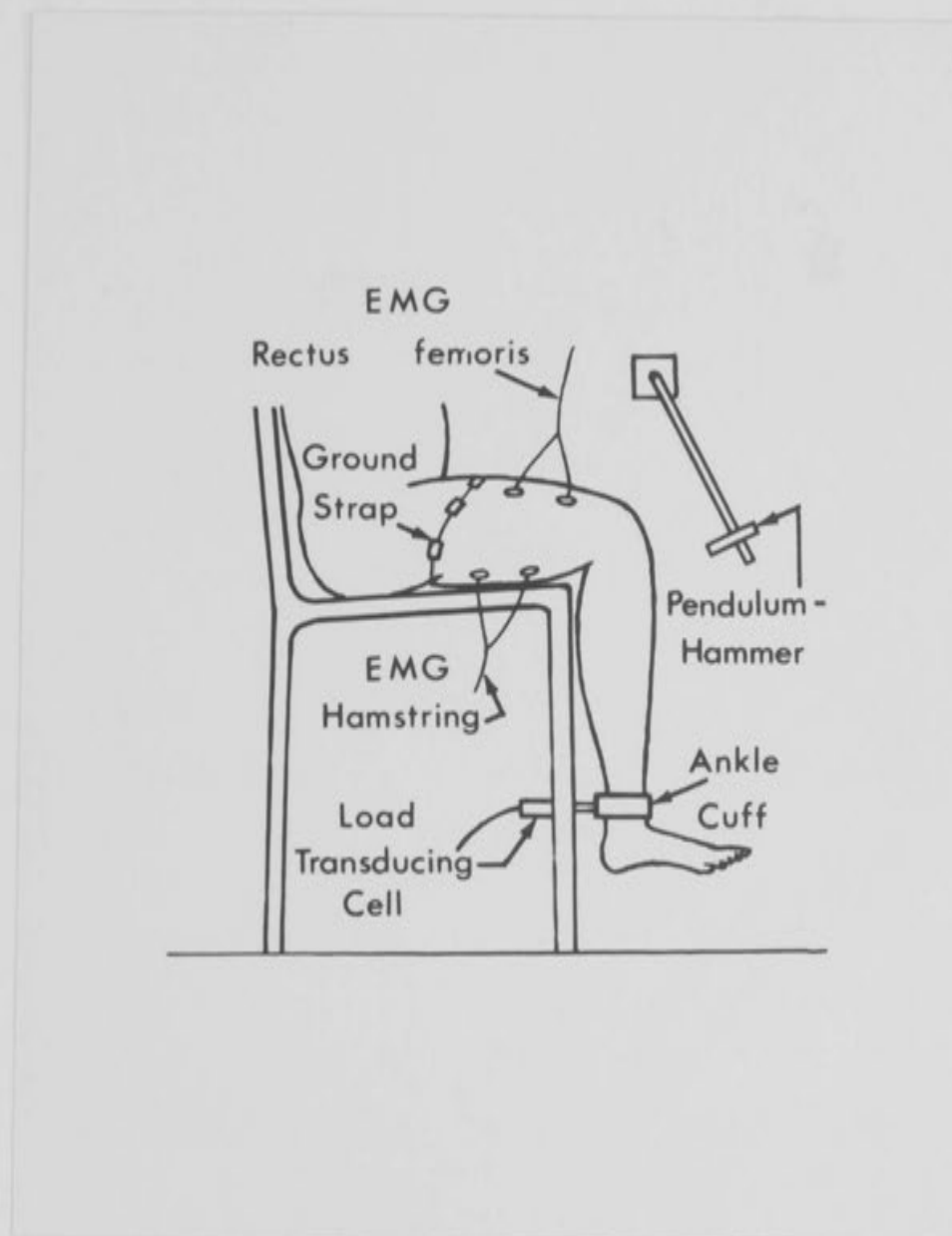


Figure 4

Sketch to show the general experimental arrangement for eliciting the patellar reflex and for obtaining the observations of the relevant variables. The special supports for the S's thighs are omitted for clarity.

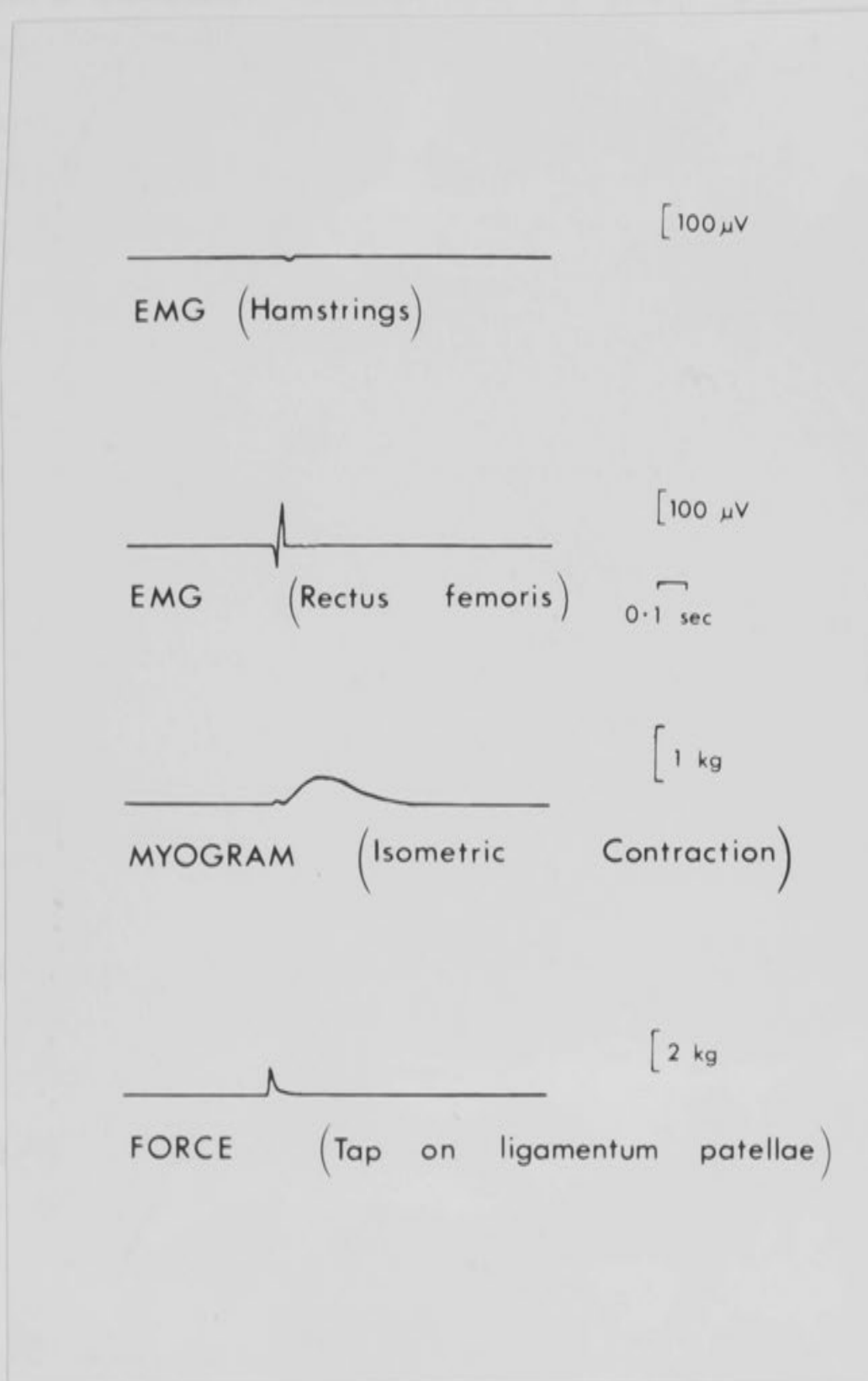


Figure 5

Simultaneous electromyogram and force records of the patellar reflex to show the responses of a S highly trained in relaxation.

The E remained inside the 'Spesti' room with the S during the experimental sessions.

The amplitude-time relations of the independent variable (tap on the ligament), and the dependent variables (electrical and mechanical aspects of the reflex response) were observed. Latency was not measured in this experiment because the timing trigger was not available.

The particular aspects of these variables to be investigated were:

- (a) the area under the triangular record, representing the impulse (or integral of force and time) of the tap on the ligament,
- (b) the area under the myogram, representing the impulse of the isometric contraction of the rectus femoris muscle,
- (c) the maximum height of the myogram, representing the maximum force of the isometric contraction, and
- (d) the area between the di- or tri-phasic record and the axis in the electromyogram, representing the impulse (or integral of voltage and time) of the MAP.

RESULTS

1. Independent variable

The duration of the tap on the ligamentum patellae was found to be 0.02 sec for all trials across the Ss

and, therefore, only the peak force was used as the measure of the independent variable.

Peak forces applied to the ligament to elicit the reflex were of the order of 2 kg for all Ss. The range of peak forces being: Females L.V. 1.89-2.45 kg, B.H. 1.62-2.31 kg and M.D. 1.22-2.24 kg. Males G.B. 1.10-3.13 kg, W.R. 1.49-3.91 kg, R.R. 1.29-2.10 kg and A.M. 1.62-3.18 kg.

Two types of session were conducted; those in which the pendulum-hammer was dropped from a uniform height and those in which the height was varied. Under the former condition, the most commonly observed result was slight variation in the peak force of the tap (standard deviations of the order of 0.06 kg) which implies slight changes in muscle tonus but, on a few occasions, a uniform peak force was observed over about 10 trials which implies consistent muscle tonus. Under the latter conditions, there was a change in peak force according to whether the hammer was released from a greater or lesser height. Only one change in height of release was made in each session and the two sample sets of observations which resulted displayed some slight variation within sets but no overlap between sets occurred. It was assumed that muscle tonus remained fairly consistent throughout the session; therefore, the change in force of the tap resulted in a difference in the amount of deflection of the ligament and consequently in the extension of the muscle. The maximum change in peak force of the tap when a new height was used to release the hammer was 630 g.

2. Relationship between dependent variables

Irrespective of whether the force records for the tap on the ligament indicated that (a) muscle tonus was uniform over a set of trials, (b) slight changes occurred in the tonus of the muscle over trials or (c) the muscle was extended to greater or lesser amounts by heavier or lighter taps, respectively, high positive correlation coefficients were found within sessions between:

- (i) the maximum force of the isometric contraction and the impulse of the isometric contraction,
- (ii) the impulse of the isometric contraction and the impulse of the MAP, and
- (iii) the maximum force of the isometric contraction and the impulse of the MAP.

The product-moment correlation coefficients and 99 per cent confidence limits for the population parameter are given in Table I.

Data for five sessions are given for each S in the Table but these correlation coefficients were confirmed repeatedly in future experiments and in this experiment where more than five sessions were conducted with some Ss. The relationship between these pairs of variables was linear for all subjects. Figures 6, 7 and 8 show the correlation plots for one S to illustrate the linearity.

TABLE I
 DATA TO SHOW THE MEANS, STANDARD DEVIATIONS AND PRODUCT-MOMENT CORRELATIONS RELATING TO
 THE MAXIMUM FORCE OF THE ISOMETRIC REFLEX CONTRACTION, IMPULSE OF THE ISOMETRIC
 REFLEX CONTRACTION AND THE IMPULSE OF THE MUSCLE ACTION POTENTIAL.

| Subject | N | Maximum Force of Isometric Contraction(c) | | Impulse of Isometric Contraction(s) | | Impulse of Muscle Action Potential(j) | | Product-moment Correlations and 99% Confidence Limits for $r_{(pop)}$ | | | | | | | | |
|---------|----|---|-------|-------------------------------------|-------|---------------------------------------|-------|---|--------------|----------|--------------|----------|--------------|-------|-------|-------|
| | | (kg) | | (g sec) | | (uV sec) | | r_{cm} | Conf. Limits | r_{ej} | Conf. Limits | r_{cj} | Conf. Limits | | | |
| | | \bar{X} | S_x | \bar{X} | S_x | \bar{X} | S_x | | | | | | | | | |
| B.H. | 10 | 0.28 | 0.20 | 56.2 | 41.1 | 0.51 | 0.19 | 0.997 | 0.999 | 0.979 | 0.968 | 0.995 | 0.800 | 0.978 | 0.995 | 0.885 |
| | 20 | 0.37 | 0.22 | 71.2 | 45.2 | 0.90 | 0.69 | 0.989 | 0.997 | 0.962 | 0.994 | 0.998 | 0.979 | 0.983 | 0.995 | 0.942 |
| | 18 | 0.32 | 0.15 | 65.7 | 32.7 | 0.51 | 0.23 | 0.989 | 0.997 | 0.959 | 0.946 | 0.985 | 0.775 | 0.963 | 0.990 | 0.880 |
| | 10 | 0.27 | 0.18 | 48.0 | 40.8 | 0.39 | 0.55 | 0.986 | 0.998 | 0.906 | 0.975 | 0.992 | 0.915 | 0.939 | 0.991 | 0.880 |
| | 10 | 0.45 | 0.47 | 89.4 | 87.4 | 0.84 | 0.67 | 0.999 | 0.999 | 0.993 | 0.985 | 0.997 | 0.900 | 0.988 | 0.998 | 0.918 |
| L.V. | 25 | 1.07 | 0.59 | 218.2 | 120.1 | 1.79 | 1.11 | 0.993 | 0.998 | 0.978 | 0.985 | 0.995 | 0.954 | 0.980 | 0.993 | 0.940 |
| | 20 | 0.79 | 0.48 | 140.4 | 74.1 | 0.59 | 0.29 | 0.979 | 0.994 | 0.928 | 0.926 | 0.945 | 0.901 | 0.966 | 0.990 | 0.890 |
| | 10 | 0.89 | 0.28 | 167.4 | 45.3 | 0.84 | 0.32 | 0.993 | 0.999 | 0.952 | 0.972 | 0.996 | 0.820 | 0.934 | 0.990 | 0.620 |
| | 10 | 0.62 | 0.31 | 114.2 | 51.1 | 0.39 | 0.24 | 0.995 | 0.999 | 0.965 | 0.955 | 0.993 | 0.720 | 0.969 | 0.996 | 0.810 |
| | 10 | 0.49 | 0.13 | 92.0 | 22.2 | 1.59 | 0.30 | 0.984 | 0.997 | 0.890 | 0.927 | 0.989 | 0.580 | 0.881 | 0.982 | 0.380 |
| M.D. | 10 | 0.55 | 0.25 | 96.4 | 43.3 | 0.38 | 0.29 | 0.992 | 0.998 | 0.945 | 0.928 | 0.989 | 0.509 | 0.946 | 0.992 | 0.880 |
| | 10 | 1.22 | 0.44 | 205.8 | 73.9 | 1.51 | 0.53 | 0.982 | 0.997 | 0.880 | 0.987 | 0.998 | 0.912 | 0.982 | 0.997 | 0.880 |
| | 10 | 0.56 | 0.44 | 99.4 | 60.4 | 1.48 | 1.10 | 0.999 | 0.999 | 0.993 | 0.976 | 0.996 | 0.840 | 0.969 | 0.996 | 0.810 |
| | 9 | 0.67 | 0.21 | 133.8 | 80.9 | 0.44 | 0.24 | 0.989 | 0.998 | 0.913 | 0.978 | 0.997 | 0.830 | 0.976 | 0.996 | 0.780 |
| | 10 | 1.11 | 0.85 | 181.4 | 126.7 | 1.54 | 1.19 | 0.986 | 0.998 | 0.906 | 0.919 | 0.988 | 0.550 | 0.927 | 0.989 | 0.580 |
| R.B. | 15 | 0.57 | 0.39 | 98.7 | 72.5 | 1.74 | 1.47 | 0.992 | 0.998 | 0.965 | 0.979 | 0.995 | 0.890 | 0.975 | 0.994 | 0.890 |
| | 21 | 1.01 | 0.51 | 199.8 | 107.4 | 2.34 | 1.41 | 0.985 | 0.996 | 0.950 | 0.991 | 0.997 | 0.970 | 0.964 | 0.989 | 0.890 |
| | 17 | 0.76 | 0.58 | 142.6 | 110.3 | 1.08 | 0.91 | 0.964 | 0.991 | 0.860 | 0.886 | 0.971 | 0.630 | 0.941 | 0.986 | 0.780 |
| | 10 | 1.04 | 0.49 | 210.8 | 96.6 | 1.49 | 0.90 | 0.936 | 0.990 | 0.620 | 0.959 | 0.994 | 0.750 | 0.984 | 0.997 | 0.890 |
| | 10 | 2.25 | 0.75 | 427.0 | 130.3 | 6.14 | 1.30 | 0.979 | 0.995 | 0.885 | 0.903 | 0.985 | 0.470 | 0.942 | 0.992 | 0.660 |
| V.R. | 19 | 0.71 | 0.26 | 103.8 | 35.8 | 2.28 | 0.60 | 0.939 | 0.983 | 0.800 | 0.909 | 0.974 | 0.707 | 0.857 | 0.958 | 0.570 |
| | 20 | 1.61 | 0.38 | 227.9 | 45.4 | 1.63 | 0.59 | 0.926 | 0.978 | 0.760 | 0.928 | 0.979 | 0.770 | 0.861 | 0.958 | 0.590 |
| | 26 | 1.02 | 0.37 | 172.4 | 53.9 | 3.55 | 0.57 | 0.959 | 0.986 | 0.880 | 0.904 | 0.968 | 0.757 | 0.904 | 0.966 | 0.740 |
| | 12 | 0.55 | 0.19 | 60.9 | 27.5 | 2.95 | 0.23 | 0.926 | 0.986 | 0.640 | 0.930 | 0.987 | 0.670 | 0.854 | 0.971 | 0.370 |
| | 27 | 0.58 | 0.36 | 79.4 | 64.6 | 2.94 | 0.61 | 0.983 | 0.994 | 0.952 | 0.975 | 0.991 | 0.932 | 0.980 | 0.993 | 0.944 |
| A.M. | 33 | 2.11 | 0.94 | 276.7 | 105.1 | 2.10 | 1.37 | 0.985 | 0.994 | 0.962 | 0.979 | 0.992 | 0.949 | 0.985 | 0.994 | 0.962 |
| | 25 | 1.75 | 0.72 | 269.3 | 115.2 | 3.19 | 0.81 | 0.974 | 0.991 | 0.924 | 0.890 | 0.962 | 0.702 | 0.882 | 0.958 | 0.680 |
| | 25 | 1.85 | 0.70 | 255.9 | 89.9 | 1.84 | 0.95 | 0.992 | 0.997 | 0.976 | 0.960 | 0.986 | 0.885 | 0.965 | 0.988 | 0.900 |
| | 14 | 2.75 | 0.86 | 394.6 | 113.1 | 2.02 | 0.93 | 0.988 | 0.997 | 0.944 | 0.977 | 0.995 | 0.885 | 0.968 | 0.993 | 0.860 |
| | 30 | 0.92 | 0.48 | 118.7 | 60.0 | 0.76 | 0.46 | 0.989 | 0.996 | 0.971 | 0.955 | 0.983 | 0.880 | 0.955 | 0.983 | 0.880 |
| G.B. | 16 | 1.80 | 0.36 | 300.1 | 46.8 | 3.88 | 1.10 | 0.971 | 0.993 | 0.880 | 0.946 | 0.986 | 0.789 | 0.949 | 0.989 | 0.800 |
| | 37 | 2.65 | 0.49 | 371.3 | 69.8 | 2.65 | 0.93 | 0.939 | 0.974 | 0.860 | 0.935 | 0.973 | 0.850 | 0.965 | 0.985 | 0.917 |
| | 35 | 1.97 | 0.55 | 324.3 | 69.1 | 1.94 | 0.75 | 0.949 | 0.979 | 0.880 | 0.875 | 0.949 | 0.730 | 0.952 | 0.981 | 0.880 |
| | 32 | 1.86 | 0.38 | 303.1 | 66.7 | 1.33 | 0.51 | 0.919 | 0.968 | 0.800 | 0.882 | 0.952 | 0.716 | 0.938 | 0.976 | 0.850 |
| | 11 | 0.77 | 0.35 | 112.3 | 57.3 | 0.66 | 0.34 | 0.974 | 0.996 | 0.850 | 0.931 | 0.988 | 0.635 | 0.957 | 0.993 | 0.760 |

Correlation plot to show the linear relationship between the impulse of the MAF and the maximum force of the isometric contraction. $r = 0.993$, $N = 20$, Subject B.H.

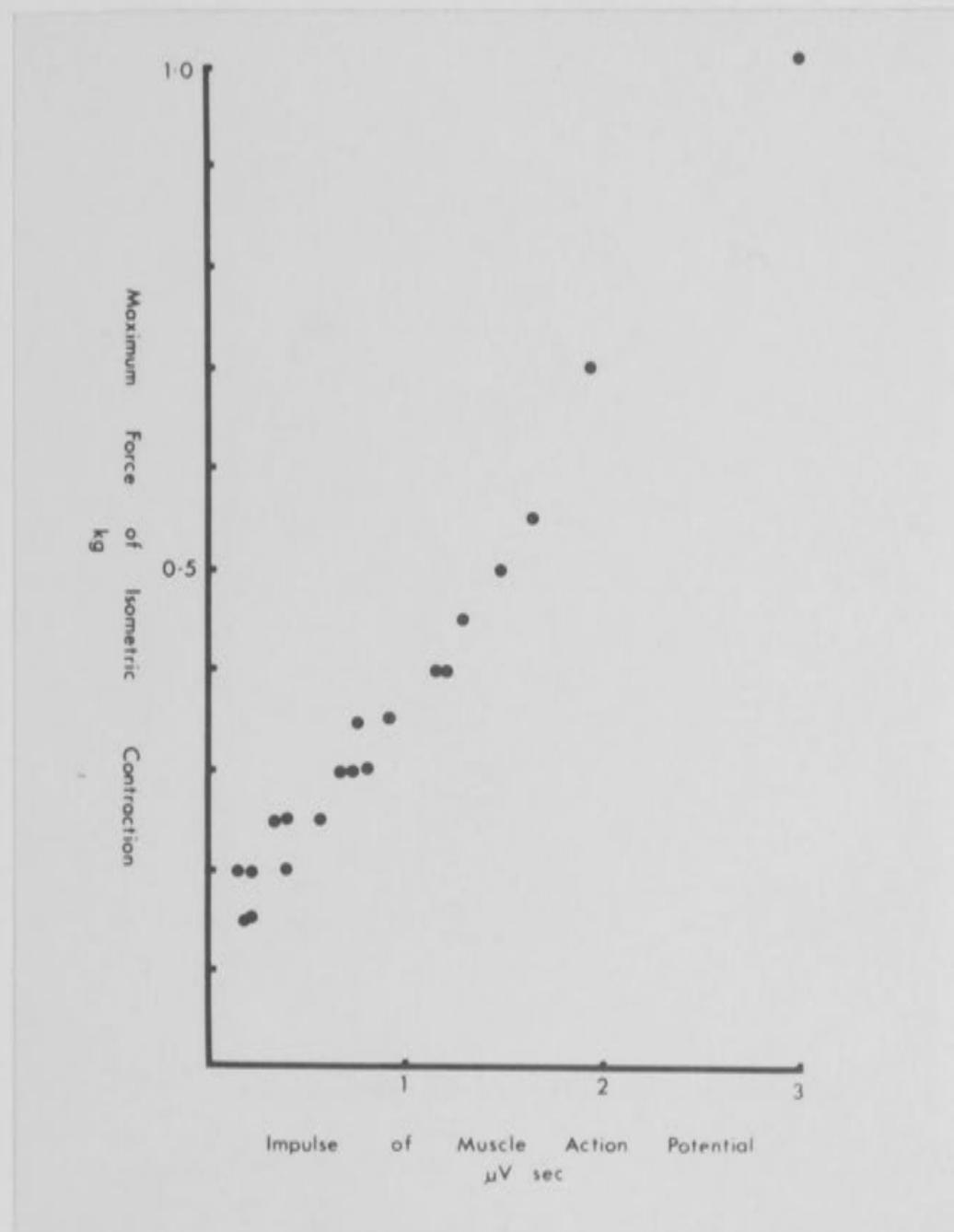


Figure 6

Correlation plot to show the linear relationship between the impulse of the MAP and the maximum force of the isometric contraction. $r = 0.983$, $N = 20$, Subject B.H.

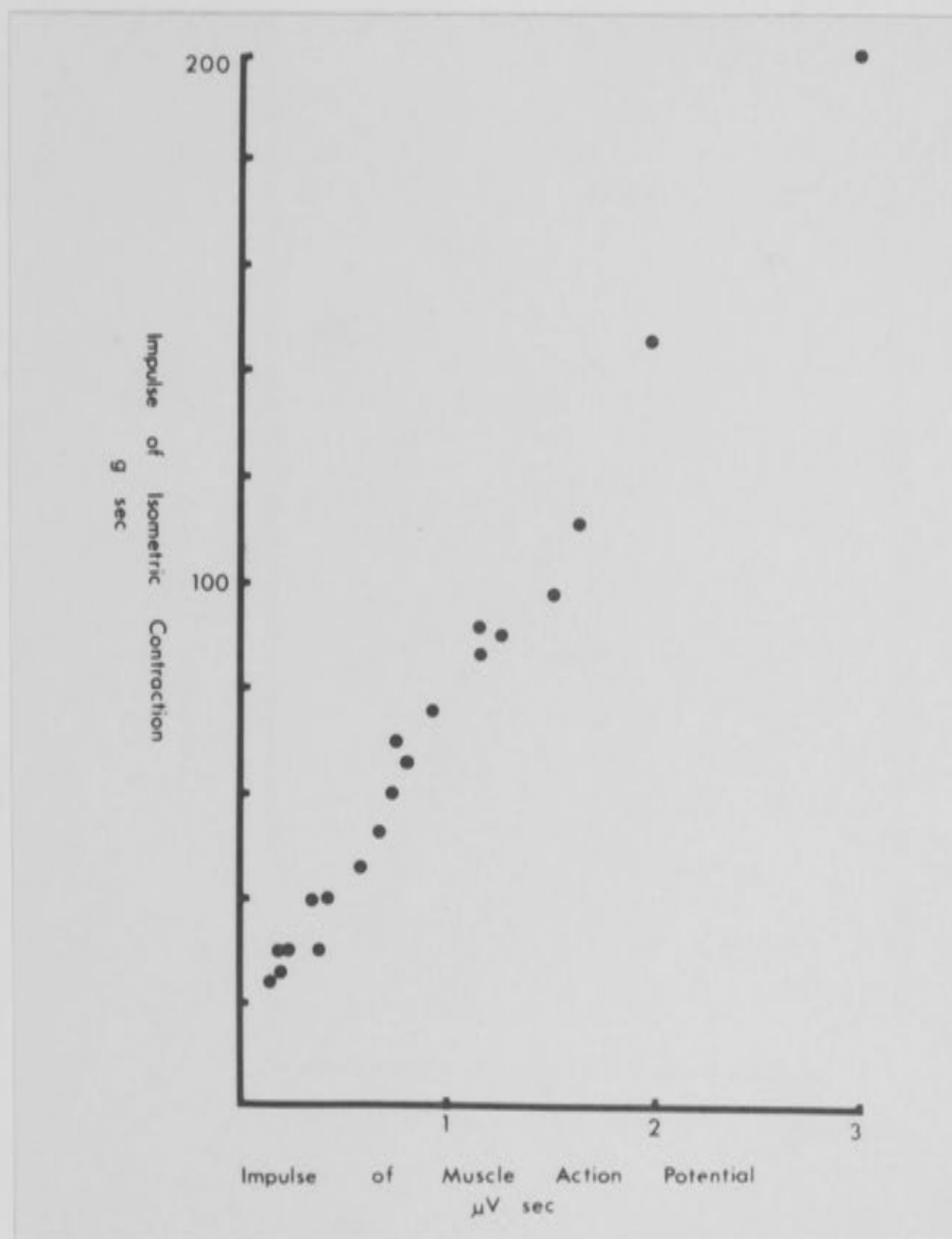


Figure 7

Correlation plot to show the linear relationship between the impulse of the MAP and the impulse of the isometric contraction. $r = 0.994$, $N = 20$, Subject B.H.

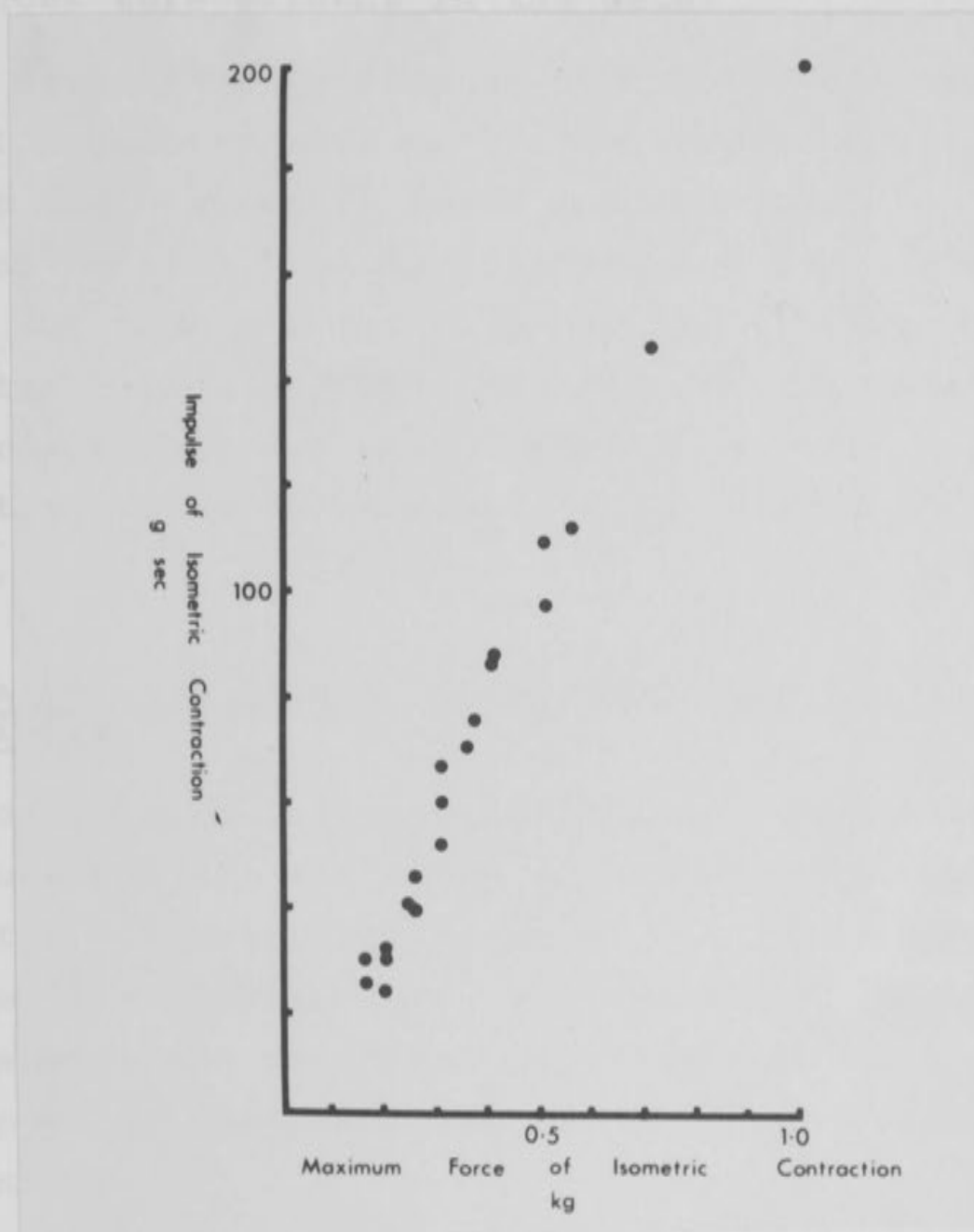


Figure 8

Correlation plot to show the linear relationship between the maximum force of the isometric contraction and the impulse of the isometric contraction.
 $r = 0.989$, $N = 20$, Subject B.H.

Small standard deviations were obtained in the three variables (Table I) for all Ss. No sex differences were evident in the data.

An associated finding was that, for all Ss, two temporal sequences were most consistent. First, the time for the myogram to reach maximum height (contraction time) was approximately 0.1 sec and, second, the time for the rise and fall of the myogram (hereafter called the response time of the myogram) was approximately 0.4 sec (Figure 9). These observations were independent of the height of the myogram.

3. Relationship between independent and dependent variables

Because high positive correlation coefficients were found between the three dependent variables, any one of the variables may be used as a valid index of the isometric contraction. The impulse of the MAP was chosen as the principal dependent variable for the purpose of comparing the stimulus and response relationship.

It was found that, within a session, each S could maintain consistent muscle tonus over short periods involving about ten taps, often in succession. Even with a uniform stimulus, slightly variable responses resulted. Since the correlation coefficient between stimulus and response is zero, under these conditions, the mean, standard deviation and range of the impulse of the MAP are given below for sessions in which the peak force on the ligament was consistent over a

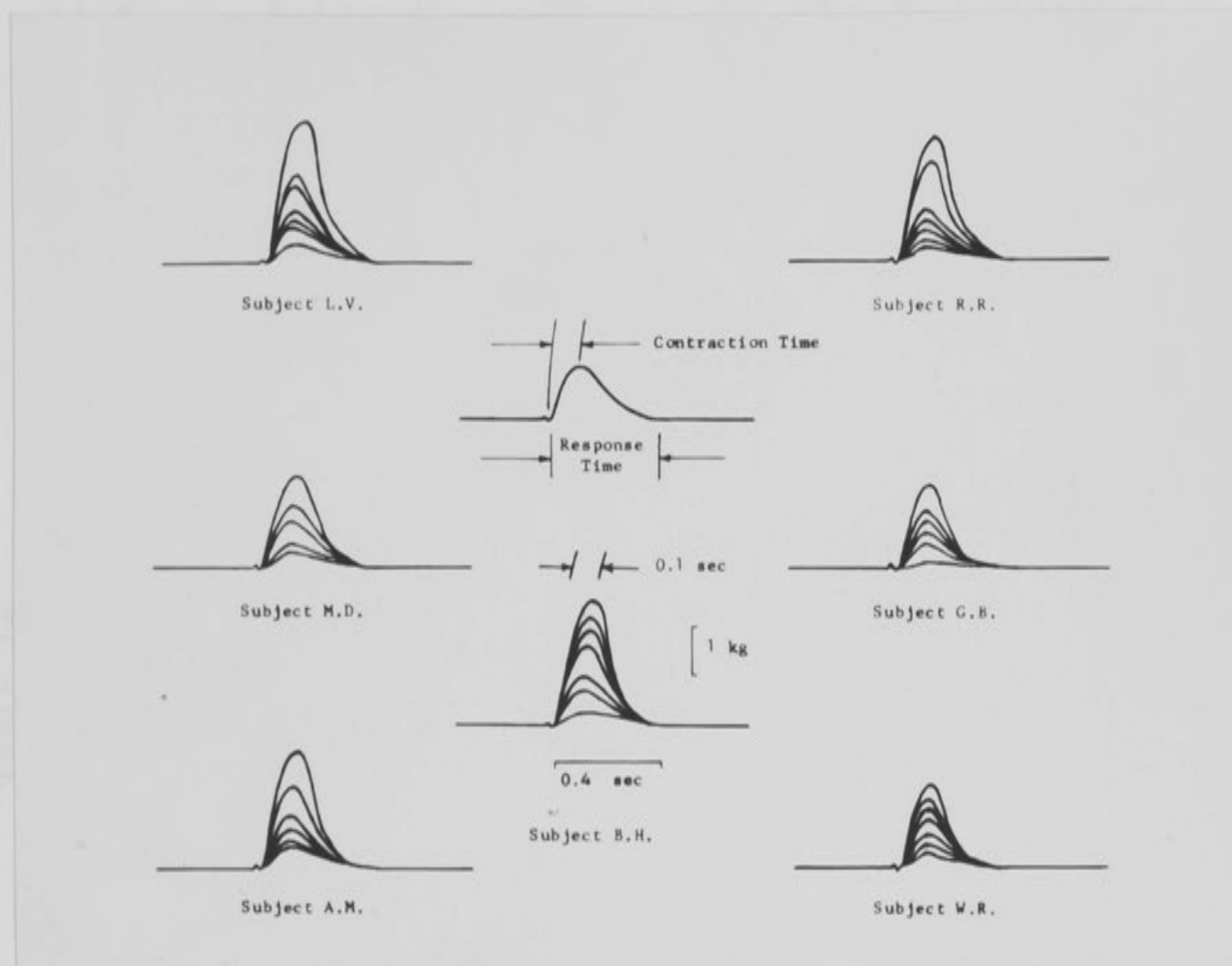


Figure 9

Superimposed traces for all Ss of the myograms of the isometric contraction in a mechanically elicited patellar reflex. The contraction time and response time are consistent irrespective of the height of the myogram. Jendrassik augmentation was used in some trials with each S to spread the amplitude of the responses.

number of trials and the pendulum-hammer was dropped from a uniform height.

TABLE Ia

| Subject | Uniform Peak force of tap on ligament (kg) | Number of trials | Impulse of Muscle Action Potential (μ V sec) | | |
|---------|--|------------------|---|------|-----------|
| | | | \bar{x} | S | Range |
| B.H. | 2.03 | 10* | 0.52 | 0.29 | 0.10-1.01 |
| | 2.03 | 10 | 0.76 | 0.44 | 0.20-1.63 |
| L.V. | 2.38 | 10 | 2.12 | 1.35 | 0.72-4.97 |
| | 2.38 | 10* | 1.23 | 0.30 | 0.65-1.56 |
| M.D. | 2.24 | 8 | 1.25 | 0.46 | 0.52-2.16 |
| | 2.17 | 6* | 1.87 | 1.07 | 0.71-3.44 |
| R.R. | 1.96 | 7 | 2.17 | 1.01 | 1.17-4.03 |
| | 1.49 | 7 | 0.93 | 0.74 | 0.20-2.44 |
| W.R. | 3.43 | 8* | 3.50 | 0.57 | 2.86-4.88 |
| | 2.50 | 10* | 2.39 | 0.21 | 2.12-2.78 |
| A.M. | 2.94 | 9* | 3.36 | 0.86 | 1.76-4.49 |
| | 3.18 | 10* | 3.18 | 0.78 | 2.08-4.29 |
| G.B. | 3.13 | 10* | 3.51 | 0.36 | 2.78-4.03 |
| | 2.18 | 10* | 1.29 | 0.35 | 0.91-2.08 |

* indicates successive trials in the experimental session.

The standard deviation of the dependent variable was less than $1 \mu V$ sec in eleven of the fourteen sessions.

When muscle tonus varied slightly between trials within a session (which was the more general observation), as indicated by variations in the peak force of the tap on the ligament even when the pendulum-hammer was released from a uniform height, the correlations between the stimulus and response, almost without exception, were not significantly different from zero.

An example for each S of the product-moment correlation between the variables as well as the mean, standard deviation and range of each variable, is given in Table Ib.

Finally, in some sessions, the force of the tap on the ligament was altered by changing the height from which the pendulum-hammer was dropped. Only one such change was made in a session, the height sometimes being increased and sometimes decreased so that the ligament was deflected either more or less than previously. For each height there was a range of peak force on the ligament and a range of response, measured by the impulse of the MAP. Irrespective of the force of the tap on the ligament, the correlation coefficient between the dependent variables was high and positive (Table Ic).

TABLE Ib

| Subject | Number of trials | Peak force of tap on ligament (a) | | | Impulse of Muscle Action Potential (j) | | | Product-moment Correlation r_{aj} |
|---------|------------------|-----------------------------------|------|-----------|--|------|-----------|-------------------------------------|
| | | \bar{x} | S | Range | \bar{x} | S | Range | |
| B.H. | 10 | 1.95 | 0.04 | 1.89-2.03 | 1.19 | 0.51 | 0.47-2.14 | 0.093 |
| L.V. | 10 | 1.97 | 0.02 | 1.89-2.03 | 0.84 | 0.32 | 0.52-1.47 | 0.598 |
| M.D. | 10 | 2.11 | 0.06 | 2.03-2.17 | 0.68 | 0.16 | 0.51-1.10 | 0.373 |
| R.R. | 10 | 1.35 | 0.05 | 1.29-1.42 | 0.96 | 0.49 | 0.26-1.82 | 0.507 |
| W.R. | 10 | 1.66 | 0.07 | 1.49-1.76 | 0.48 | 0.29 | 0.15-1.06 | 0.548 |
| A.M. | 10 | 1.80 | 0.09 | 1.69-1.89 | 2.99 | 1.17 | 0.78-4.68 | 0.728* |
| G.B. | 10 | 1.69 | 0.05 | 1.62-1.76 | 1.71 | 0.43 | 0.61-2.16 | 0.304 |

* Significantly different from zero ($p < 0.05$).

TABLE Ic

| Subject | Session | N | Peak force of the tap on ligament (kg) | | | Impulse of MAP (μ V sec) | | | Prod.-moment Correlation, Impulse of Iso, Cont. and Impulse of MAP |
|---------|---------|----|--|------|-----------|----------------------------------|-------------------|-----------|--|
| | | | \bar{x} | S | Range | \bar{x} | S | Range | |
| G.B. | 1 | 16 | 3.09 | 0.07 | 2.94-3.13 | 3.54 | 0.42 ^a | 2.86-4.29 | 0.876 |
| | | 21 | 2.17 | 0.04 | 2.03-2.18 | 1.97 | 0.59 | 0.45-3.25 | 0.915 |
| | | 37 | | | | 2.64 | 0.96 ^a | 0.45-4.29 | 0.935 |
| | 2 | 25 | 2.86 | 0.08 | 2.81-2.94 | 2.20 | 0.69 | 1.04-4.05 | 0.967 |
| | | 10 | 2.18 | 0.00 | 2.18-2.18 | 1.29 | 0.35 ^b | 0.91-2.08 | 0.893 |
| | | 35 | | | | 1.94 | 0.74 ^b | 0.91-4.05 | 0.875 |
| A.M. | 1 | 17 | 2.36 | 0.09 | 2.18-2.54 | 1.02 | 0.45 ^c | 0.52-2.21 | 0.931 |
| | | 16 | 2.93 | 0.07 | 2.81-3.13 | 3.25 | 1.05 | 0.97-4.94 | 0.959 |
| | | 33 | | | | 2.10 | 1.37 ^c | 0.52-4.94 | 0.979 |
| | 2 | 15 | 1.99 | 0.14 | 1.89-2.03 | 0.75 | 0.52 | 0.20-1.84 | 0.962 |
| | | 15 | 2.28 | 0.11 | 2.17-2.45 | 0.76 | 0.38 ^d | 0.20-1.53 | 0.979 |
| | | 30 | | | | 0.76 | 0.46 ^d | 0.20-1.84 | 0.955 |

F ratio between the variances:

- a F = 5.16 (p < 0.001)
- b F = 4.53 (p < 0.01)
- c F = 9.38 (p < 0.001)
- d F = 1.42 (p is N.S.)

These data also indicate that combining the observations within a session for the two sets of conditions of muscle extension did not affect the high positive correlation between the mechanical and electrical aspects of the dependent variable (right hand column, Table Ic).

DISCUSSION

The general results of this experiment indicate that satisfactory control can be achieved over the environmental and organismic variables which affect the reflex response. The variance of the dependent variables is small and, thus, the principal aim of the experiment has been accomplished. The small standard deviations found in each of the dependent variables (Table I) testify to the efficacy of the methods used to control the response.

(a) Stimulus-response relationships

There were three different sets of conditions which were observed in the experiments in regard to the stimulus (tap on the ligament) and response (impulse of the MAP) relationships. First, equal muscle tonus and uniform stimuli (Table Ia); second, slight variations in muscle tonus and corresponding slight variations in stimuli (Table Ib); and third, experimentally produced changes in stimuli with slight variations in muscle tonus (Table Ic). Each of these three conditions will be examined in turn.

(i) Equal muscle tonus and uniform stimuli

The fundamental objective with each individual was to deliver the same stimulus in each trial to a muscle having constant physical characteristics. That is, the rate and amount of muscle extension were to be the same with each tap on the ligament, and muscle tonus and spindle sensitivity were to remain uniform. The expectation, under these circumstances, was that a relationship would exist between the stimulus and response.

The results (Table Ia) show that even when the dual indices of a quiescent EMG and uniform force on the ligament (the hammer being released from the same height each trial so that the rate and amount of muscle extension was consistent) were used to assess the state of the muscle, there was a range of response (standard deviation of the impulse of the MAP being of the order of $0.60 \mu V \text{ sec}$). However, this seems a reasonable range of responses for a given stimulus in an intact, normally functioning biological system. The variance is sufficiently low to enable accurate comparisons to be made with different types of experimental treatments in future experiments.

(ii) Slight variations in muscle tonus and in stimuli

The most common observation was for slight variations (of the order of S.D. = 0.05 kg) in the peak force of the tap on the ligament when the hammer was released from a uniform height within sessions (Table Ib). This implies that muscle tonus varied

with the fluctuations in force on the ligament such that increased tone increased the tension in the ligament and a greater resistance was offered to the tap. Obviously, the deflection of the ligament (and consequently, the rate and amount of muscle extension) will vary according to the resistance offered by the ligament to the tap. Therefore, both the muscle tonus and the extension of the muscle varied in these sessions.

Under these circumstances, the correlation coefficient between the measures of the stimulus and response almost invariably, was not significantly different from zero (Table Ib). However, the standard deviations, indicated by the impulse of the MAP, were of the same order as those observed when muscle tonus was consistent (Tables Ia and Ib). Apparently, slight differences in the rate and amount of muscle extension had little effect on the variance of the impulse of the MAP compared with uniform extension between trials.

(iii) Experimentally produced changes in the force of the tap on the ligament and slight variations in muscle tonus

When the force of the tap on the ligament was altered by either increasing or decreasing the height from which the pendulum-hammer was released, the assumption was made that there would be corresponding changes in the rate and amount of muscle extension. Except on one occasion (G.B., session 2, Table Ic), there was a slight variation of muscle tonus and of

response (impulse of the MAP) within each treatment (that is, within each force range). The standard deviations for stimulus and response under each treatment were of similar magnitude to those found under similar conditions in Table Ib. However, when the responses for both treatments are pooled, a significant increase occurred in variance over that found in the single treatment with the least variance (Table Ic). Alteration in the rate and amount of muscle extension thus is an important variable contributing to the variance of the response. This is not surprising as the amount of extension determines the number of spindles which respond and the rate of extension determines the frequency of discharge.

In accounting for the results from these three aspects of the stimulus-response relationship, it seems likely that the small variance in responses when the muscle tonus is uniform and also when there are slight fluctuations in muscle tonus, is the result of attenuation of fusimotor activity. Random variations in fusimotor biasing of the intrafusal muscle fibres would cause fluctuations in the threshold of the primary ending of the spindle but this activity can occur without inducing any detectable change [that is, a change greater than about 50 mg (Matthews, 1964)] in the tension of the extrafusal fibres (Eldred and Fujimori, 1958). Presumably, this gamma discharge could have occurred when muscle

tonus was consistent as indicated by uniform forces on the ligament and, indeed, would be expected in the intact person because some degree of fusimotor tone probably is necessary for the existence of the stretch reflex (Eldred, 1960). This tonic discharge would account for the small range observed in the dependent variable by randomly changing the excitability level of the pool of spindles whose threshold was near firing for the amount of muscle extension applied.

Presumably, if fusimotor discharge could be made consistent and muscle tonus held constant, a uniform rate and amount of muscle extension between trials would result in consistent responses. These conditions are not likely to be achieved with an intact human although a significant correlation between input and output apparently is possible with long training. After five months of regular sessions a significant correlation coefficient of 0.728 ($p < 0.05$) was found with one S (A.M. Table Ib) but this was not attained again.

Uniform muscle tonus was observed only two or three times with each S over at least five months of testing and then only for short periods involving about 10 trials within a session. Apparently, perfect consistency of muscle tonus is very difficult to achieve and maintain even for a short time in normal human Ss. The more general observations were slight changes in tonus within a session. It is unlikely that fusimotor biasing of the spindles was powerful enough, under the conditions of control in this

experiment, to cause afferent discharge and thus, by exciting motoneurones, bring about slight fluctuations in muscle tonus. These alterations probably were the result of the frequent re-arrangement of the sets of extrafusal fibres that always are in a state of isometric contraction to produce muscle tone. It is thought that only a proportion of the extrafusal fibres are involved in the maintenance of tonus at any particular time and this would be true especially in these experiments where the muscle is relaxed and electrically quiescent. The number of extrafusal fibres involved varies from time to time and thus fatigue does not occur because of prolonged contraction (Johnston and Whillis, 1949). It seems that in the change from one state to another, some slight fluctuations in tonus must occur.

(b) Relationships between the dependent variables

(i) Correlations between mechanical and electrical responses

The high, significant, positive correlation coefficients and linear relationships which were found between the mechanical and electrical aspects of the reflex contraction (Table I and Figures 6, 7 and 8) do not appear to have been reported in the literature.

The early work of Adrian and Bronk (1929) on single motor units with needle electrodes, revealed that the gradation in strength of force of a voluntary contraction in man was brought about by changes in the number of muscle fibres in action and also by changes in the

frequency of discharge of the motoneurons. Since then many reports have appeared in the literature to show that surface EMG parallels voluntary muscular tension under conditions of isometric contraction. For example, Ralston et al. (1947) found a close agreement between tension and the integrated EMG during voluntary isometric contraction when amputees were used who had cineplastic tunnels placed through forearm flexor and extensor muscles. Later, Ralston combined with others (Inman, et al., 1952) to confirm this finding with normal human Ss and Lippold (1952), in a similar study, reported product-moment correlations in the range 0.935 to 0.995 and linearity of the relationship between isometric tension and integrated MAP. More recently, Close, et al. (1960) have demonstrated a linear relationship between motor unit action potential counts (electronically computed) and tension during the isometric voluntary contraction of human soleus muscle. A similar relationship would be expected between the electrical and mechanical response of human muscle during isometric reflex contraction. Buller and Dornhorst (1957) obtained records which would have given this information for the Achilles reflex but an investigation of this relationship was not the aim of their research.

In the present study, product-moment correlations in the range 0.882 to 0.994 were found between the impulse of the isometric contraction and the impulse of the MAP, and in the range 0.854 to 0.988 were

found between the maximum force of the isometric contraction and the impulse of the MAP. These correlations existed irrespective of whether there were variations in force applied to the ligament (implying significant variations in the extension of the muscle), slight variations in muscle tonus (implying slight changes in the extension of the muscle by a hammer released from uniform height), or consistent muscle tonus (implying uniform extension of the muscle). Table Ic shows that the correlations between the mechanical and electrical impulses are not affected by grouping the data from two sets of trials using forces whose ranges do not overlap.

The explanation for the close concomitance between the mechanical and electrical responses probably lies partly in the high degree of consistency which was evident in muscle tonus within sessions, partly in the fact that the muscle did not change length appreciably during contractions and partly because there was no complicating activity from the flexor (hamstring) muscles during the reflex. The indices of muscle tonus obtained from the EMG (the criterion for which was quiescence) and the force applied to the ligament by the pendulum-hammer (fairly consistent forces, i.e. standard deviation within sessions of approximately 0.05 kg, being observed for uniform heights of hammer fall) may be taken as sensitive detectors of change in the physical state of the muscle. The records obtained from these two measures are sufficiently consistent

to enable the conclusion to be made that the physical characteristics of the muscle were such that its resistance to extension did not alter in any marked way within sessions. This consistency in a fully functioning biological system may be attributed to the attenuation of sensory stimuli and the relaxed state of the S. Presumably, the decrease in centrifugal activity emanating from supra-spinal levels of the CNS, which resulted from this procedure, basically, is the reason why the muscle could be maintained in a consistent physical state. When the S is activated to an extent where the muscle is not quiescent, large fluctuations in muscle tonus are likely so that the compliance characteristics of the muscle would vary from trial to trial. Under these conditions, pooling all observations may reduce the correlation coefficient, tend to make the plot of the relationship elliptical rather than linear and increase the variance. In addition, measurement errors would increase sharply because the phasic aspect of the MAP would be embedded in background noise of the EMG and the myogram probably would exhibit clonus, making it difficult to extract the purely reflex components. The occurrence of clear records, uncontaminated with extraneous information, would seem to be essential if the relationship is to be demonstrated.

consider need to record the myogram is low. The motor unit responses are artificially with increased intensity of electrical stimulation.

(ii) Correlations between the two mechanical aspects of the response

Almost perfect product-moment correlation coefficients (range 0.919 to 0.999) have been found between the impulse and the maximum force of the isometric reflex contraction.

The explanation of this relationship between the height and area of the myogram of rectus femoris muscle may be found in the characteristics of its shape. For all Ss, irrespective of amplitude, the total duration of the isometric contraction (response time) was consistently 0.4 sec and the maximum height was reached in 0.1 sec (contraction time).

The consistency of response time and contraction time, irrespective of the height of the myogram, found in the present experiments (Figure 9) with normal human Ss is in agreement with observations on anaesthetised cats when electrical stimulation of motor neurones (in the form of a synchronous square wave pulse of 1 msec duration) was used to elicit unit twitch and muscle twitch responses (Devanandan, et al., 1965).

Close (1966), in work on animal preparations, has shown that provided the temperature and resting tension of the muscle remain constant, and the compliance of the transducer used to record the myogram is low, the motor twitch responses add arithmetically with increased intensity of brief electrical stimulation.

The time course of the various responses in the present experiment suggests that the time relations of the motor units closely resemble those for the muscle as a whole. There is no way of knowing whether the additions to the height of the myogram are single units or groups of units but, in any event, all additional motor units behave in the same way and there is a very narrow distribution of the time relations of the myogram. In fact, myograms of the same height were found to have identical shapes within sessions and often between sessions held on different days.

There is evidence that the responses most probably are twitches. First, the MAPs were discrete, diphasic spikes of 0.04 sec total duration without any obvious repetitive activity in the EMG. Therefore, the motor volley probably was highly synchronous. Second, the contraction time of 0.1 sec observed for mechanical stimulation corresponds with the contraction time for twitches in response to a brief, single shock stimulus to motor nerves in human leg muscles (Fulton, 1955; Prosser and Brown, 1961; Buller, et al., 1959). For these reasons, the responses of these intact, human Ss most probably are twitches of units or groups of units operating in parallel and adding arithmetically.

This evidence also indicates that the force-time characteristics of the reflex response were pre-programmed.

When a synchronous volley of impulses reaches the motor end-plates of the extrafusal fibres, a wave of contraction spreads over the fibres resulting in a brief twitch followed by relaxation. The electrical discharge is detected as a MAP which, in these experiments, was found to be directly related to the area under the myogram (Table I). The impulse of the MAP had a total duration of 0.04 sec and yet was directly related to a response which covered a time period ten times that of the MAP. In addition, the shape of the myograms showed a smooth contraction and relaxation (Figures 5 and 9) which indicates that the responses were not modified by rebound contraction or clonus in the relaxation phase (Creed, et al., 1932).

These features of the response make it analogous to the action of a 'ballista', the catapult-like Roman weapon used to hurl rocks. All the conditions of a ballistic response are present in the isometric reflex contraction observed in this experiment; a large, pre-set force operating for a short period produces a response which long outlasts the period of application of the force and which is not modified once it has been initiated (Walsh, 1959).

The evidence presented in Chapter II showed that activity in the fusimotor neurones cannot modify the response during a reflex. The results obtained under the conditions of environmental and organismic control in this experiment, lend support to this view. Apparently, the force-time

relationships of the isometric reflex contraction are programmed beforehand by at least such factors as the resting tension of the extrafusal fibres and the degree of bias given to the intrafusal fibres by gamma innervation. Once the response is triggered by the mechanical tap, which imparts a sudden, brief stretch to the muscle, it is not modified during its course.

However, with a S untrained in relaxation, the compliance of the muscle may not be uniform. When extension of the muscle occurs under these circumstances, a main volley of impulses, followed by others (as other extrafusal fibres are extended), would result in asynchronous motor unit discharges. Therefore, the myogram would display a small hump or humps during the relaxation phase (Creed, et al., 1932). The rebound contractions or clonus destroy the true relationship between the height and area of the myogram. There is no doubt that interpretation becomes difficult when there is ongoing motor unit activity in a muscle being investigated (Benson and Gedye, 1961) and therefore, it is most desirable to work with a S whose muscle is electrically quiescent before and immediately after the MAP.

(c) Conclusion

The three aims of the experiments have been fulfilled.

First, the conditions of control outlined in Chapter III have been shown to yield a substantial degree of consistency in the reflex response.

Second, all three dependent variables give equally reliable information about the reflex response because a close concomitance has been found between them and,

Third, highly significant, positive, linear relationships have been shown to exist between

- (i) the impulse of the MAP and the impulse of the isometric reflex contraction,
- (ii) the maximum force of the isometric contraction and the impulse of the MAP and,
- (iii) the maximum force and the impulse of the isometric contraction.

The variance of the within sessions responses was considered sufficiently low to enable future experiments to be conducted to establish the precise effects of various stimuli on the reflex response. The results of experiments designed to do this will be given in the next chapters.

CHAPTER VI

THE EFFECT OF STIMULATION OF CERTAIN SKIN AREAS
ON THE PATELLAR REFLEXRationale for the experiment

Evidence from experiments in neurophysiology indicates that the effects produced by cutaneous stimulation are among the most pronounced of the many excitatory and inhibitory influences which are involved in peripheral regulation of motoneurone discharge in the alpha and gamma pathways. Lombard (1887) seems to have been the only clinician to note the augmentation of a stretch reflex by skin stimulation in a normal human S but no precise data were presented in his paper. There seems to be good reason, therefore, to investigate the effects of stimulation of skin areas on muscle response in the intact human in an attempt to extend the findings of experimental infra-human neurophysiology to man.

Neurophysiologists have been interested in the strong functional interaction that exists between a muscle and the area of skin which covers it, the muscle being excited by a stimulus applied to its own portion of skin and inhibited from many other areas of skin. The preciseness and invariability of this reciprocal system of excitation and inhibition have been demonstrated conclusively with spinal and decerebrate infra-human animals, notably cats.

It has been known for some time that mechanical stimulation of the skin may cause muscle response (Creed, et al., 1932). Hagbarth made the first detailed study of excitatory and inhibitory ipsilateral skin areas for both flexor and extensor alpha motoneurons, demonstrating a muscle-skin organization of reflexes by using the monosynaptic method of electrical testing on decerebrate cats (Hagbarth, 1952). Different types of stimulation to the skin were used (pressure, touch, cold, warmth and heat) and the results indicate clearly that although pinching the skin is the most effective stimulus, similar results can be obtained by using the other kinds of stimuli. The general finding in Hagbarth's experiments is that muscular activity is influenced in opposite ways from different skin areas of a limb, the receptors in the skin over any particular muscle, whether flexor or extensor, facilitating the motoneurons of that muscle and inhibiting those of its antagonist.

The possible explanation for this phenomenon proposed by Hagbarth (1952) is that of a dual defense mechanism. The contraction of the muscle renders the skin over the muscle flaccid so that a noxious object should penetrate less readily and also the muscle itself becomes firm to protect underlying tissues from damage.

Whilst investigating the peripheral mechanisms and reflex function of muscle stretch receptors, Hunt (1952) discovered that reflex activity in small

(gamma) efferent fibres, which in mammals exclusively innervate the intrafusal fibres of muscle spindles, can be increased by excitation of a variety of afferent fibres from the skin as well as from the muscle. About the same time Granit, Job and Kaada (1952) published a paper which related the pinna reflex with both the gamma efferent discharge and muscle spindle afferent activity. Touching the animal's ear frequently evoked strong gamma excitation so that often the intrafusal muscle fibres were co-activated to a degree which neutralised the unloading of the muscle spindle by extrafusal contraction. Even when the muscles did not contract when the ear was touched, excitation of gamma efferents and spindle afferents was shown to occur.

At this stage, there was a need for information about the functional relationship between gamma and alpha activity in skin reflexes. Research by Eldred and Hagbarth (1954) looked at the correlation between the large and small diameter efferent activity. The influence of skin stimulation by pinching without disturbing the underlying muscle was studied in the gastrocnemius and tibialis anterior muscles (representing an extensor-flexor pair) of spinal cats. The influence of the skin reflexes upon the fusimotor fibres and alpha fibres was similar; activity was facilitated from the skin over the responding muscle and inhibited from some other areas especially the foot. Without exception, the alpha and gamma fibres from a given skin area were affected similarly. However, the fusimotor fibres were found

to have a much lower threshold to skin stimulation than the alpha fibres. These experiments were confirmed by the work of Hunt and Paintal (1958) who found that touching the skin provided an especially important and effective way of regulating fusimotor activity. One of their observations, which is of particular relevance for the present experiment, was that stimulation of the skin overlying quadriceps increased the discharge in fusimotor neurones to that muscle but stimulation of the skin over the hamstring muscle decreased the background discharge.

The above findings make it obvious that the efferent channels involved in reflexes initiated by skin stimulation are well known but knowledge of the afferent pathways from the skin is deficient (Lloyd, 1960). However, it seems that impulses from cutaneous sources project to dorsal column nuclei (Perl, et al., 1962) and then to the medial reticular formation (Wolstencroft, 1961). Connections to the reticular formation explain why the fusimotor system is activated when skin is stimulated.

The general conclusions from experiments with infra-human animals on the effect of skin stimulation on reflexes are that (a) muscle and the skin which overlie it are functionally integrated, (b) there is a relationship between the activity in alpha and gamma efferents to a particular muscle, these fibres being co-excited or co-inhibited, (c) there is a strict reciprocal organisation of skin reflexes, the receptors in the skin over any particular muscle

(whether extensor or flexor) facilitating the motoneurons supplying that muscle and inhibiting those of its antagonist and (d) there is evidence that pathways from cutaneous receptors lead to the reticular formation.

Hagbarth (1952) has pointed out that his observations on the excitatory and inhibitory skin areas for extensor and flexor motoneurons are of clinical interest. He hastened to add that the results of his animal experiments cannot be applied directly to man but they suggest the possibility of similar mechanisms.

The aim of the present experiment was to discover whether a similar organisation of reflexes exists in the intact human by investigating the effect of skin stimulation on the patellar reflex.

METHOD

Subjects

Three young adult males (age range 19 to 26 years) in good health were used for the experiments. They had participated in a previous experiment and therefore had practised for at least 20 hours (in separate one hour sessions) the technique of mental and muscular relaxation developed by Jacobson (1924).

Testing was not begun unless the following criteria were achieved for the EMG from rectus femoris, (a) quiescence before and also immediately following the tap to the ligamentum patellae, and (b) discrete,

highly synchronous di- or tri-phasic MAPs in response to the brief stretch stimulus.

The EMG from the hamstrings was expected to show negligible activity throughout. The Ss were asked to maintain a consistent level of moderate activity as far as possible outside the experimental sessions because quiescent EMGs were not possible after very little sleep or strenuous physical activity.

The force of the tap on the ligament was adjusted in each session for the particular S so that it was just over the threshold necessary to elicit a brisk reflex. The interval between the taps was at least 15 seconds to allow the S to return to a relaxed state before the next trial.

Time of day for testing was held constant for each individual S. In all cases, the right patellar reflex was investigated by isometric recording of the response. The Ss wore an eye mask and the illumination was reduced to a low level to aid relaxation. The mask also prevented S observing the operations conducted by E who behaved as silently as possible.

Apparatus

The items of apparatus were as previously described except that the U-shaped support for the right thigh was modified by cutting a narrow slot so that the skin over the hamstring muscle could be scratched without difficulty.

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The items of apparatus were as previously described except that the U-shaped support for the right thigh was modified by cutting a narrow slot so that the skin over the hamstring muscle could be scratched without difficulty.

Experimental design

Only within-sessions comparisons were made between control and experimental treatments because of large parameter changes between sessions which could complicate between-sessions comparisons. The level of the responses of individual Ss would alter between sessions for reasons such as the following:

- (a) changes in skin resistance and electrode contact would affect the reception of EMG signals,
- (b) differences in muscle tonus would not only alter the level of the responses but also affect the variance, and
- (c) day to day fluctuations in the threshold of sensitivity of the spindle receptors would result in corresponding changes in force applied to the ligament to elicit a reflex.

In addition, individual differences in muscle tonus and the geometry of the knee-joint would result in differences between Ss in the rate and amount of muscle extension for a given deflection of the ligament.

For these reasons, only comparisons between means within sessions were made. In all cases two-tailed t-tests were used between control and experimental observations.

Experimental sessions consisted of 5 normal trials with the S relaxing (Condition A); 10 trials with

conditions as for A but with a scratch being administered to the skin over the belly of the quadriceps muscle beginning 2 seconds before the tap and continuing while the tap was made on the ligamentum patellae (Condition B); and finally, 5 normal trials (Condition A). This ABA design enabled compensation to be made for possible changes over time by considering the 10 trials under condition A as one sample of observations and the 10 trials under condition B as another sample set.

Subsidiary experiments were added to a number of the main sessions to test the effect of scratching the skin over the hamstrings and the medial side of the foot (over the abductor hallucis muscle). The same temporal sequence of scratch of the skin and tap of the ligament was used as for the quadriceps tests.

The sequence of normal, scratch (quadriceps) and scratch (hamstrings or foot) was varied within sessions to test for possible sequential effects of the type of treatment.

In all cases the skin over the muscles of the ipsilateral limb was stimulated and the intensity of the scratch (which was made by uniform hand pressure using the end of a piece of 1/16" diameter wire) was sufficient to cause a slight erythema of the skin.

It was predicted that scratching the skin over the quadriceps muscle would augment the reflex whilst scratching the skin over the hamstrings or tibialis muscles would diminish the response.

RESULTS

Data collection

One aspect of the independent variable (the maximum force of the tap on the ligamentum patellae) and four aspects of the dependent variable (the maximum force of the isometric reflex contraction, the impulse of the isometric reflex contraction, the impulse of the MAP from rectus femoris and the latency) were observed.

Some data were rejected because statistical tests for the significance of the difference between the means of the force of the tap under normal and experimental conditions showed that a difference beyond chance existed. Since the pendulum-hammer was released from a uniform height within sessions, these significance-test results indicate that changes occurred in the resting tension of the muscle between treatments and therefore no conclusions could be reached concerning the dependent variables for such sessions. On this criterion 7 sessions yielded usable results with one S (G.B.) and 5 sessions each with the other two Ss (A.M. and W.R.). Table II gives the data for each S.

TABLE II
THE MEANS, STANDARD DEVIATIONS AND THE RESULTS OF t -TESTS FOR THE SIGNIFICANCE OF THE DIFFERENCE BETWEEN MEANS FOR THE MEASURES OF THE INDEPENDENT AND DEPENDENT VARIABLES WITHIN SESSIONS.
NO [NORMAL TRIALS]; SC (Q) [SCRATCH TRIALS FOR QUADRICEPS]; SC (H) [SCRATCH TRIALS FOR HAMSTRINGS]; SC (F) [SCRATCH TRIALS FOR MEDIAL SIDE OF FOOT].

| SUBJECT | SESSION SEQUENCE | TREATMENT | INDEPENDENT VARIABLE | | | | | | | | | | | | | | DEPENDENT VARIABLES | | | | | | | | | | | | | |
|---------|------------------|-----------|--|-------|------|----|---|-------|---------|----|--|-----------|-------|---------|--|---------|---------------------|-------|---------------------------------|----|---------|----------------|----------------|---------|----|--|--|--|--|--|
| | | | MAXIMUM FORCE OF TAP ON THE LIGAMENTUM PATELLAE (kg) | | | | MAXIMUM FORCE OF ISOMETRIC CONTRACTION (kg) | | | | IMPULSE OF ISOMETRIC CONTRACTION (g sec) | | | | ELECTRICAL IMPULSE EMG (QUADRICEPS) (μV sec) | | | | LATENCY PATELLAR REFLEX (m sec) | | | | | | | | | | | |
| | | | \bar{x} | s | t | df | \bar{x} | s | t | df | F | \bar{x} | s | t | df | F | \bar{x} | s | t | df | F | | | | | | | | | |
| 1 | NO | SC (Q) | 1.559 | 0.032 | 0.46 | 17 | 1.214 | 0.345 | 2.79* | 17 | 3.66* | 191.0 | 67.6 | 2.47* | 17 | 4.25* | 3.32 | 1.232 | 2.95** | 17 | 1.03 | 18.15 | 0.261 | 4.82*** | 17 | | | | | |
| | | | 1.396 | 0.045 | | | 1.879 | 0.660 | | | | 312.8 | 139.3 | | | | | 5.01 | 1.251 | | | | 16.94 | 0.236 | | | | | | |
| 2 | NO | SC (Q) | 2.044 | 0.101 | 1.45 | 18 | 0.978 | 0.142 | 3.96*** | 18 | 2.42 | 120.5 | 22.6 | 4.43*** | 18 | 1.79 | 0.457 | 0.118 | 3.09** | 18 | 8.90** | 20.55 | 0.492 | 4.77*** | 18 | | | | | |
| | | | 2.100 | 0.095 | | | 1.314 | 0.225 | | | | 173.5 | 30.3 | | | | | 0.813 | 0.345 | | | | 19.42 | 0.564 | | | | | | |
| 3 | NO | SC (Q) | 2.331 | 0.071 | 0.21 | 18 | 1.298 | 0.426 | 3.82** | 18 | 1.32 | 215.5 | 45.7 | 4.10*** | 18 | 2.05 | 1.236 | 0.677 | 3.37** | 18 | 1.17 | 20.41 | 0.386 | 2.65* | 18 | | | | | |
| | | | 2.338 | 0.077 | | | 2.087 | 0.491 | | | | 319.0 | 65.4 | | | | | 2.301 | 0.733 | | | | 19.88 | 0.503 | | | | | | |
| G.B. 4 | NO | SC (Q) | 2.387 | 0.243 | 0.19 | 18 | 1.520 | 0.317 | 2.24* | 18 | 3.51* | 229.5 | 44.0 | 2.26* | 18 | 4.47* | 0.784 | 0.182 | 2.31* | 15 | 4.74* | 20.08 | 0.489 | 3.99*** | 18 | | | | | |
| | | | 2.418 | 0.350 | | | 1.995 | 0.592 | | | | 303.0 | 93.1 | | | | | 1.158 | 0.397 | | | | 19.27 | 0.417 | | | | | | |
| 511 | NO | SC (H) | 1.920 | 0.450 | 0.13 | 8 | 1.720 | 0.569 | 1.29 | 8 | 6.60* | 290.0 | 104.0 | 1.63 | 8 | 7.83* | 1.948 | 0.712 | 1.28 | 8 | 3.07 | 18.68 | 0.276 | 0.00 | 8 | | | | | |
| | | | 1.946 | 0.052 | 1.80 | 8 | 1.352 | 0.221 | 2.40* | 8 | 3.27 | 215.0 | 37.1 | 3.17* | 8 | 3.58 | 1.520 | 0.406 | 1.89 | 8 | 5.32 | 18.68 | 0.276 | 3.53** | 8 | | | | | |
| 111 | NO | SC (Q) | 1.892 | 0.041 | | | 1.830 | 0.400 | | | | 326.0 | 70.2 | | | | 2.382 | 0.898 | | | | 17.96 | 0.364 | | | | | | | |
| | | | 1.854 | 0.030 | 1.16 | 8 | 0.800 | 0.187 | 1.58 | 8 | 3.50 | 129.0 | 25.9 | 1.73 | 8 | 1.55 | 0.440 | 0.117 | 2.28 | 8 | 1.23 | 20.00 | 0.000 | 0.73 | 6 | | | | | |
| 64 | NO | SC (F) | 1.828 | 0.041 | 1.70 | 8 | 0.950 | 0.076 | 3.03* | 8 | 58.0*** | 151.0 | 32.3 | 2.42* | 8 | 78.2*** | 0.618 | 0.129 | 3.24* | 8 | 43.4*** | 20.16 | 0.375 | 2.37* | 8 | | | | | |
| | | | 1.866 | 0.030 | | | 2.000 | 0.241 | | | | 461.8 | 285.6 | | | | | 1.870 | 0.853 | | | | 19.58 | 0.436 | | | | | | |
| 111 | NO | SC (F) | 1.532 | 0.035 | 1.81 | 8 | 0.888 | 0.428 | 3.78** | 13 | 2.83 | 136.0 | 61.6 | 3.66** | 8 | 1.46 | 1.758 | 0.845 | 19.7*** | 8 | 1.05 | 20.5 | 0.000 | 0.71 | 3 | | | | | |
| | | | 1.560 | 0.000 | 0.00 | 8 | 1.546 | 0.254 | 6.29*** | 13 | 4.27 | 295.0 | 74.4 | 3.29* | 8 | 10.9* | 3.918 | 0.822 | 5.94*** | 8 | 1.74 | 20.0 | 1.500 | 1.84 | 6 | | | | | |
| 111 | NO | SC (Q) | 1.560 | 0.000 | | | 2.786 | 0.525 | | | | 599.8 | 203.0 | | | | 6.654 | 0.624 | | | | 18.6 | 0.317 | | | | | | | |
| | | | 1.462 | 0.127 | 0.53 | 17 | 1.451 | 0.297 | 5.64*** | 18 | 4.74* | 237.0 | 49.6 | 5.94*** | 18 | 2.63 | 1.165 | 0.239 | 4.69*** | 18 | 4.96* | 18.58 | 0.286 | 0.86 | 17 | | | | | |
| 1 | NO | SC (Q) | 1.651 | 0.096 | | | 2.709 | 0.647 | | | | 414.5 | 80.4 | | | | 2.028 | 0.533 | | | | 18.45 | 0.400 | | | | | | | |
| | | | 2.058 | 0.032 | 0.47 | 18 | 1.203 | 0.454 | 1.64 | 18 | 4.19* | 183.5 | 69.9 | 1.46 | 18 | 3.38* | 0.488 | 0.216 | 1.65 | 17 | 9.98** | 19.67 | 0.634 | 3.13** | 17 | | | | | |
| 2 | NO | SC (Q) | 2.044 | 0.089 | | | 1.740 | 0.932 | | | | 250.5 | 128.5 | | | | 0.850 | 0.680 | | | | 18.96 | 0.340 | | | | | | | |
| | | | 2.336 | 0.135 | 0.70 | 13 | 1.423 | 0.455 | 2.15* | 13 | 3.37 | 238.8 | 73.1 | 3.21** | 13 | 3.35 | 0.690 | 0.258 | 1.40 | 13 | 7.09* | 20.05 | 0.466 | 1.82 | 13 | | | | | |
| A.R. 3 | NO | SC (Q) | 2.350 | 0.117 | | | 2.163 | 0.835 | | | | 322.1 | 134.0 | | | | 1.054 | 0.686 | | | | 19.51 | 0.602 | | | | | | | |
| | | | 2.156 | 0.028 | 0.57 | 8 | 1.204 | 0.187 | 8.94*** | 8 | 2.28 | 182.0 | 29.4 | 9.82*** | 8 | 2.28 | 0.608 | 0.351 | 6.93*** | 8 | 3.13 | 21.02 | 0.407 | 2.87* | 8 | | | | | |
| 4 | NO | SC (Q) | 2.170 | 0.045 | | | 2.186 | 0.123 | | | | 323.0 | 19.5 | | | | 1.564 | 0.268 | | | | 20.36 | 0.314 | | | | | | | |
| | | | 1.826 | 0.073 | 0.61 | 8 | 1.326 | 0.383 | 0.70 | 8 | 5.96 | 194 | 51.1 | 0.87 | 8 | 1.41 | 2.116 | 0.567 | 0.67 | 8 | 1.09 | 21.15 | 1.150 | 1.93 | 3 | | | | | |
| 511 | NO | SC (H) | 1.800 | 0.053 | 0.44 | 8 | 1.194 | 0.157 | 2.41* | 8 | 8.97* | 168 | 43.1 | 2.78* | 8 | 2.28 | 1.882 | 0.543 | 2.26* | 8 | 2.12 | 22.43 | 0.387 | 6.17** | 4 | | | | | |
| | | | 1.814 | 0.049 | | | 1.728 | 0.471 | | | | 265 | 65.1 | | | | | 2.836 | 0.790 | | | | 19.53 | 0.714 | | | | | | |
| 1 | NO | SC (Q) | 1.892 | 0.041 | 0.90 | 18 | 0.270 | 0.141 | 8.59*** | 18 | 12.5*** | 43.0 | 22.8 | 8.39*** | 18 | 10.8*** | 0.285 | 0.147 | 6.40*** | 18 | 25.5*** | 23.93 | 0.450 | 3.42** | 15 | | | | | |
| | | | 1.818 | 0.254 | | | 1.680 | 0.500 | | | | 250.6 | 74.8 | | | | | 1.834 | 0.749 | | | | 23.03 | 0.178 | | | | | | |
| V.B. 2 | NO | SC (Q) | 2.310 | 0.062 | 2.03 | 18 | 0.150 | 0.084 | 5.27*** | 18 | 39.9*** | 16.5 | 9.8 | 5.35*** | 18 | 52.2*** | 0.440 | 0.290 | 3.99*** | 18 | 17.5*** | NOT AVAILABLE* | | | | | | | | |
| | | | 2.247 | 0.073 | | | 1.045 | 0.529 | | | | 136.8 | 70.4 | | | | | 2.018 | 1.215 | | | | | | | | | | | |
| 3 | NO | SC (Q) | 1.866 | 0.031 | 1.91 | 18 | 0.250 | 0.100 | 3.78** | 18 | 22.0*** | 30.8 | 13.8 | 4.26*** | 18 | 19.4*** | 0.681 | 0.302 | 4.12*** | 18 | 12.9*** | 23.08 | 0.465 | 2.34* | 14 | | | | | |
| | | | 1.826 | 0.058 | | | 0.820 | 0.467 | | | | 114.5 | 60.5 | | | | | 2.094 | 1.090 | | | | 22.35 | 0.672 | | | | | | |
| 4 | NO | SC (F) | 2.268 | 0.018 | 0.61 | 8 | 0.150 | 0.114 | 1.93 | 8 | 3.92 | 16.0 | 11.8 | 1.93 | 8 | 6.02 | NOT AVAILABLE* | | | | | | NOT AVAILABLE* | | | | | | | |
| | | | 2.226 | 0.017 | | | 0.370 | 0.225 | | | | 43.2 | 29.1 | | | | | | | | | | | | | | | | | |
| 5 | NO | SC (F) | 1.854 | 0.030 | 0.99 | 8 | 0.30 | 0.110 | 1.19 | 8 | 10.7* | 35.6 | 16.9 | 1.39 | 8 | 17.6** | 0.87 | 0.291 | 1.82 | 8 | 5.36 | 23.00 | 0.500 | 2.03 | 7 | | | | | |
| | | | 1.828 | 0.052 | | | 0.50 | 0.358 | | | | 80.8 | 70.7 | | | | | 2.06 | 0.673 | | | | 22.42 | 0.360 | | | | | | |

Probability levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
* Data not available because of fault in recording apparatus.

Excitatory effects of stimulating the skin over the responding muscle

A scratch administered to the skin over the quadriceps (rectus femoris) muscle just before and during the tap on the ligamentum patellae had the effect of augmenting the force of the isometric reflex response and of shortening reflex latency (Table II). This augmentation was not the result of a general arousal caused by a scratch stimulus to the skin since scratching other areas of the ipsilateral limb did not give similar results. Figures 10 and 11 illustrate the clear effects which occurred in two of the dependent variables under normal and scratch conditions using the ABA design. Figure 12 shows two successive trials for Subject A.M. to show the changes that occurred from conditions A to B.

The main effects of augmentation of the reflex and shortening the latency were uniform and well maintained. In fact, in each of four dependent variables in the 17 sessions conducted with the three Ss, 53 of the 59 two-tailed t -tests for the significance of the difference between means yielded a probability of < 0.05 . Even when statistical significance was not achieved in a few cases (notably with Subject A.M.) the observations, without exception, were in the predicted direction.

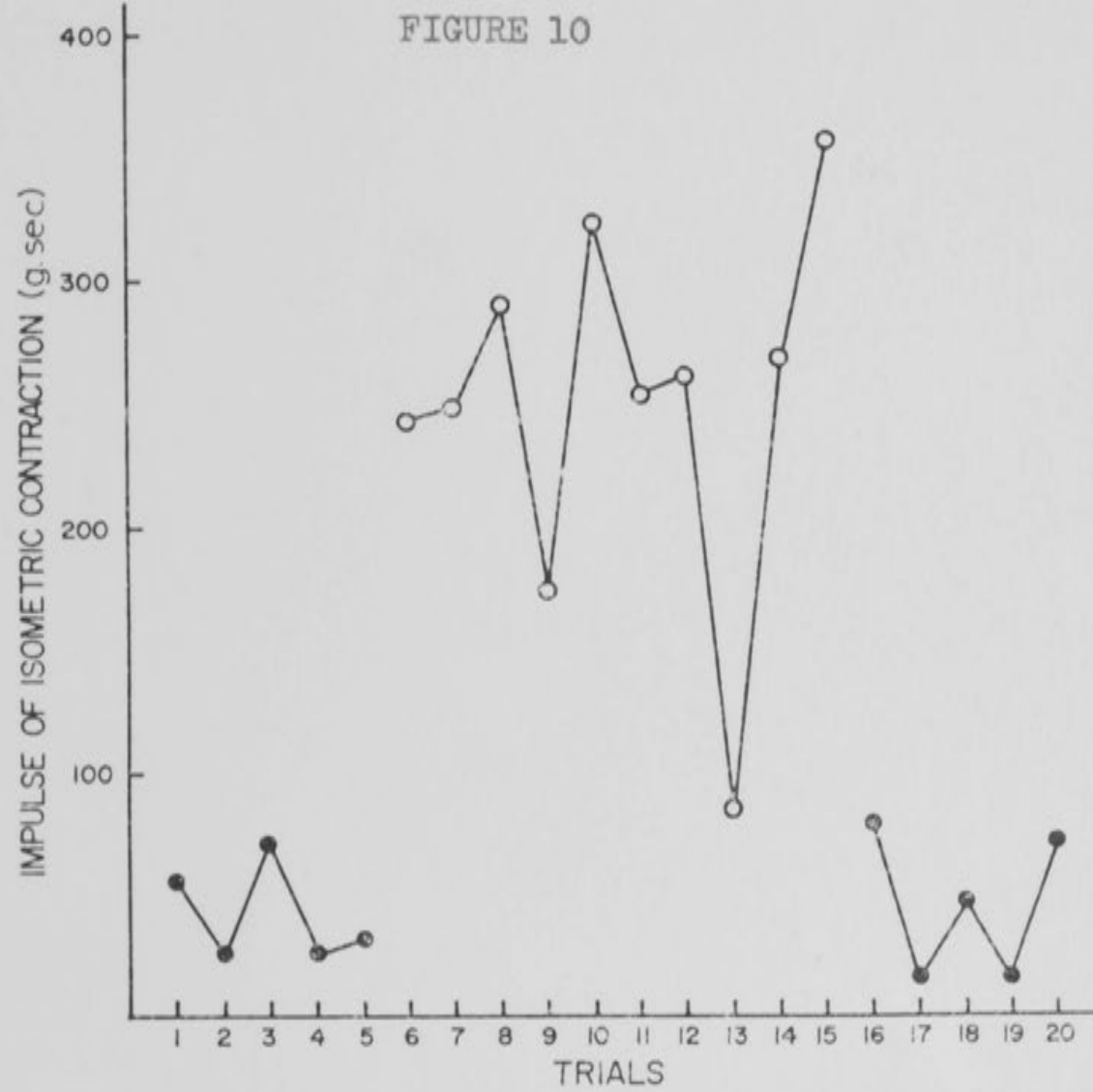


Fig. 2

Measures of the impulse of the reflex isometric contraction (subject W.R., session 2) using the ABA experimental design. ●, normal trials; ○, scratch trials, ipsilateral quadriceps.

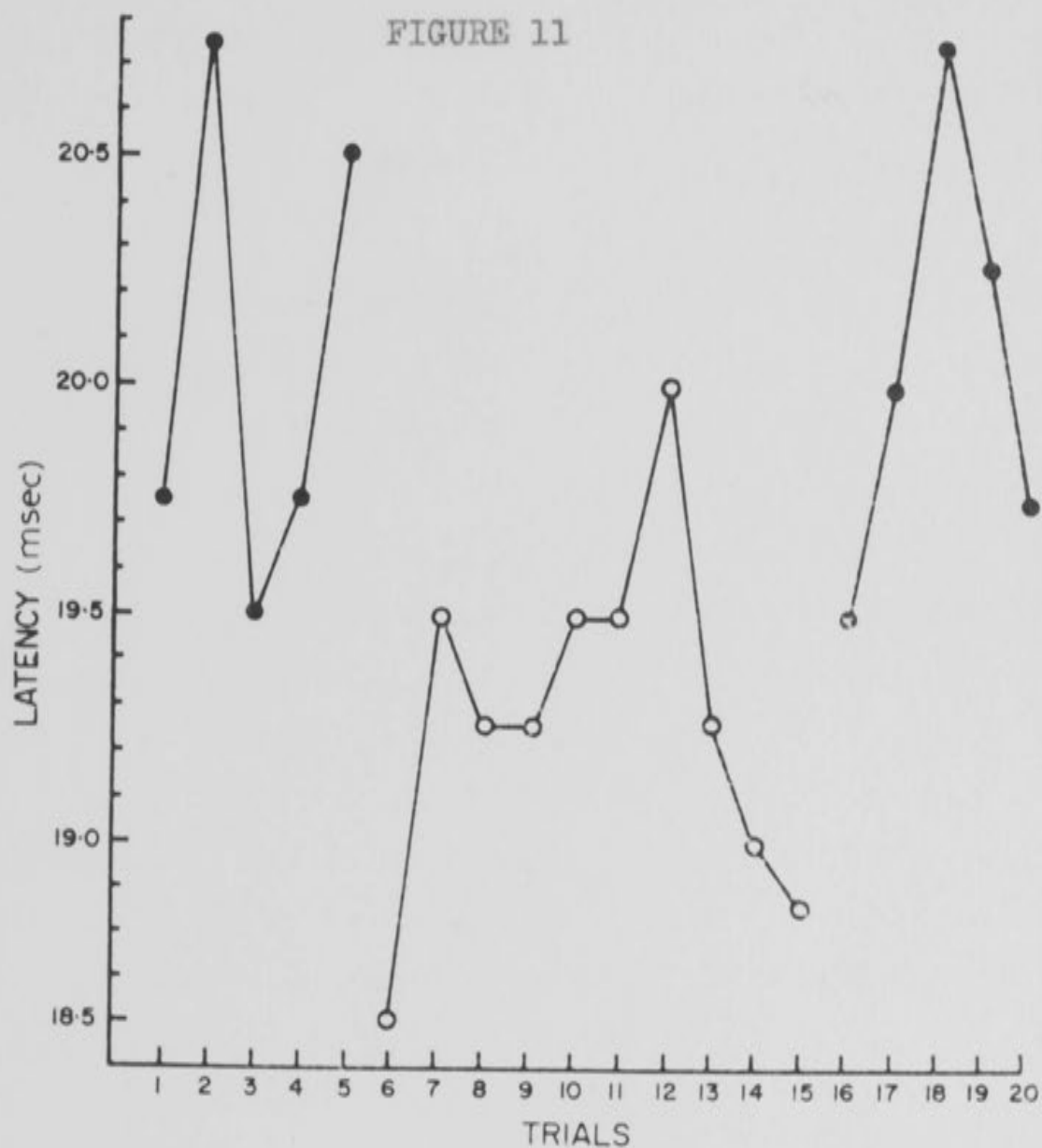


Fig. 3

Latency measures for the patellar reflex (subject G.B., session 4) using the ABA experimental design. ●, normal trials; ○, scratch trials, ipsilateral quadriceps.

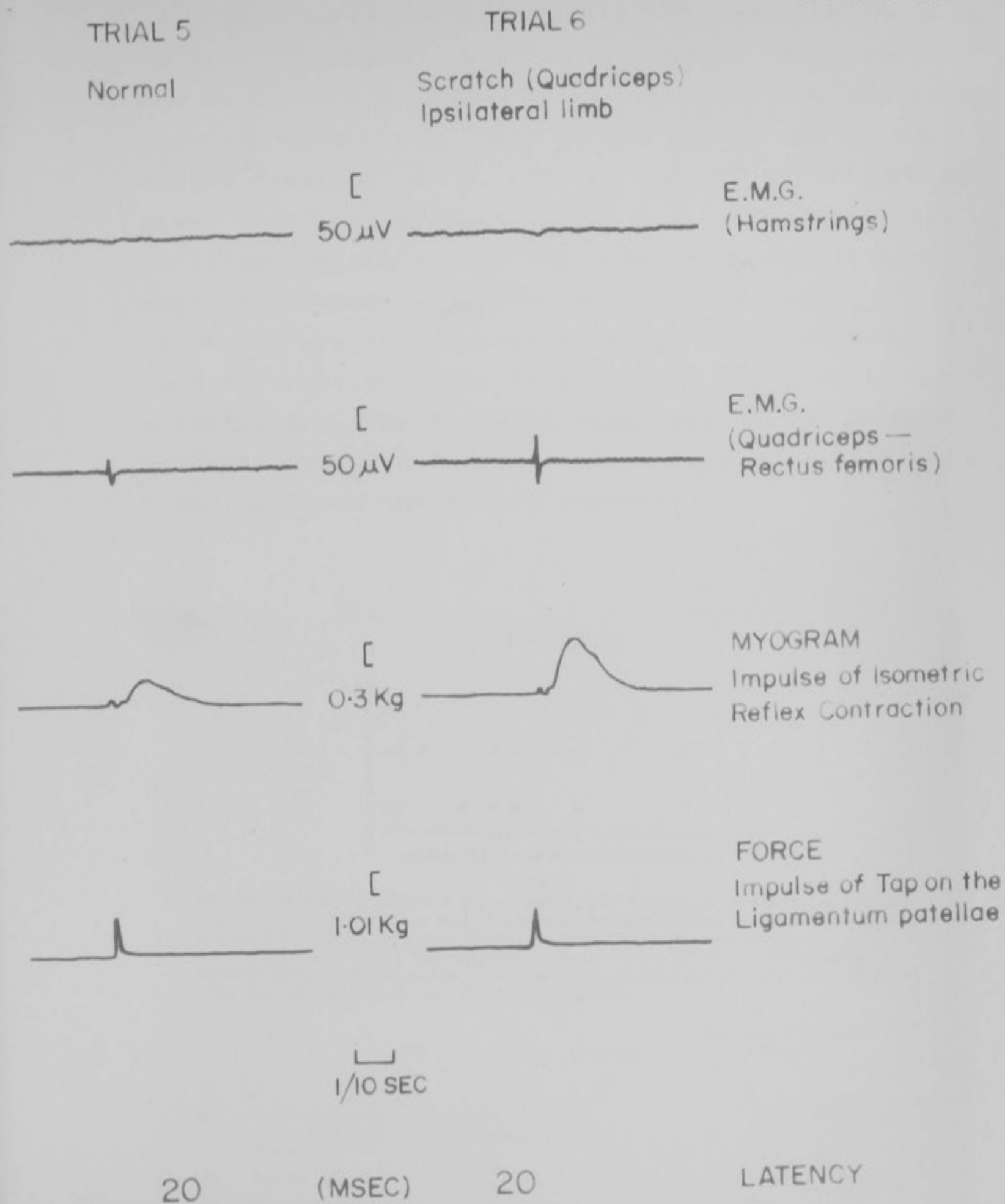
The data for Session 2, Subject A.M., provide information relating to the validity of the measures of latency. In this session latency was the only observation of the four measures of the dependent variable to show a significant difference between means. This result indicates that the shortened latency occurring concurrently with an augmented isometric reflex contraction in the other sessions, was not an artifact of the situation.

The data presented in Table II indicate the effects obtained with a uniform peak force between treatments within sessions for the tap on the ligamentum patellae. However, two questions can be asked, the answers to which yield further quantitative information about the effect of skin stimulation on the reflex. First, how much increase in the peak force on the ligament is required under Condition A (Normal trials with S relaxing) to elicit a response of similar magnitude to that obtained under Condition B (Quadriceps scratch trials) with a 'normal' tap? Second, how much decrease in the peak force on the ligament is required under Condition B to elicit a similar response to that obtained under Condition A with a 'normal' tap?

Figure 12
(next page)

Simultaneous force and EMG records for two successive trials under control (left) and the experimental treatment of a scratch on the skin over the ipsilateral quadriceps muscle prior to the tap on the ligament (right). Subject A.M.

FIGURE 12



Some trials were conducted with each of the 3 Ss to find the answer to these questions. The results for Ss G.B., W.R. and A.M. respectively, to the first question were 210 g., 400 g. and 250 g. and to the second question 340 g., 300 g. and 300 g. Figure 13 gives detailed information for G.B. Unfortunately, it is not possible with the apparatus used to know what differences in amount and rate of muscle extension are represented by these force records. Such information would be much more informative but, nevertheless, the absolute magnitude of the changes in force required indicate the strong effect of skin stimulation on the reflex response.

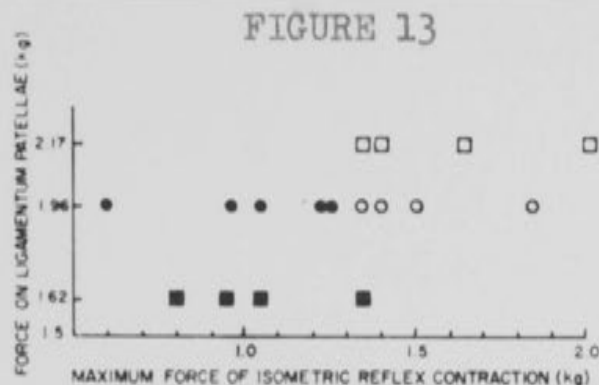


Fig. 5

The graph indicates the differences in magnitude of force expended on the ligamentum patellae (subject G.B.) to elicit maximum forces of isometric contraction matching those of conditions (A) and (B). The criteria for these observations of the dependent variable were that there should be a significant difference between responses under conditions (A) and (B) whereas there should be no significant difference between responses under conditions (A) and (C), and (B) and (D). The statistics below show that these criteria were fulfilled in the experiment.

| Treatment | Symbol | Max. force of isometric contraction | | | |
|--|--------|-------------------------------------|-------|----------|----|
| | | \bar{x} | s | P | df |
| (C) Scratch (quadriceps) but force of tap reduced so that contraction was equal to normal response | ■ | 1.04 | 0.187 | } N.S. | 7 |
| (A) Normal condition | ● | 1.02 | 0.240 | | |
| (B) Scratch (quadriceps) | ○ | 1.52 | 0.231 | } < 0.02 | 7 |
| (D) Normal but force of tap increased so that contraction was equal to scratch (quadriceps) response | □ | 1.60 | 0.257 | | |

Inhibitory effects of stimulating the skin over either the antagonist muscle or the medial side foot over the abductor hallucis

In no experiment did the effect of scratching the skin over the hamstring or abductor hallucis muscles cause any augmentation of the response. In general there was no change between the two treatments but in one session (G.B. Session 7, Figure 14) the scratch administered to the skin over the abductor hallucis

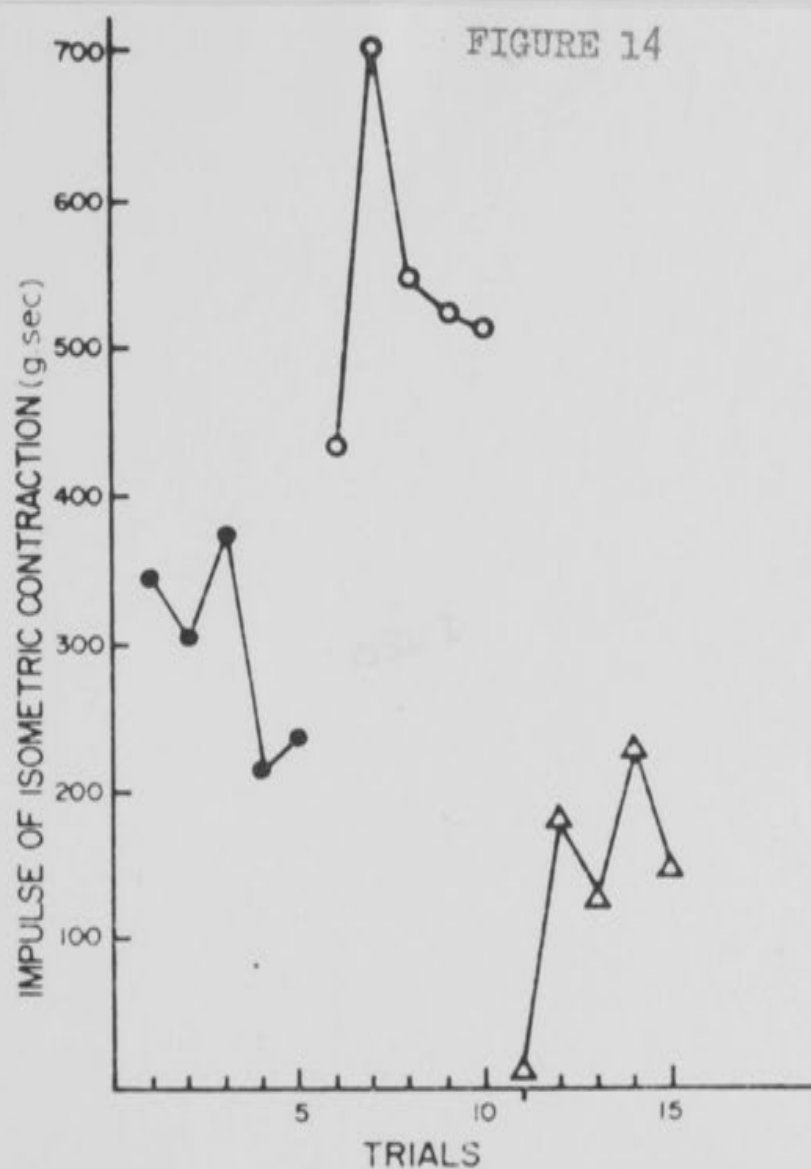


Fig. 6

Measures of the impulse of the isometric reflex contraction (subject G.B.) under normal and two experimental conditions. ●, normal trials; ○, scratch trials, ipsilateral quadriceps; and △, scratch trials, ipsilateral abductor hallucis.

muscle of the foot did inhibit the response. In that session, the peak force on the ligament was small ($p < 0.001$, 8df) compared with the other session, 6, when this effect was tested and the lighter tap may have resulted in the effects of inhibitory influences being more pronounced.

DISCUSSION

These experiments provide strong evidence for facilitation of the motoneurons supplying the rectus femoris muscle in a phasic stretch reflex when the skin over that extensor muscle is stimulated by scratching whereas the response is mostly not affected but sometimes inhibited by stimulation of skin over either the hamstrings or the abductor hallucis muscle.

The peak force on the patellar ligament did not change significantly within sessions and it can be assumed that muscle tone remained fairly constant for each particular session. However, changes in the MAP impulse indicate that there was a significant increase in the number of extrafusal muscle fibres responding when the skin over quadriceps was scratched. This increase in alpha motoneurone activity above the normal level, therefore, is not the result of recruitment at the periphery by greater stretch of the extrafusal fibres but may be reasonably assumed to be generated centrally by excitatory influences entering the alpha route (Figure 1) from cutaneous pathways.

However, Eldred and Hagbarth (1954) have shown that alpha and gamma efferents are always co-excited or co-inhibited in skin reflexes so that the fusimotor

influence on the muscle spindle must be taken into account in these experiments. The total extension applied to the primary ending of the muscle spindle is a function of the resting length of the extrafusal muscle fibres (muscle tonus) and the extension produced by the intrafusal muscle fibres brought about by fusimotor activity. The gamma, small fibre ($3-8\mu$) activation, conducting at velocities in the range 16-47 m/sec, is too slow to monitor immediately the phasic stretch involved in a tap on the ligament; the alpha, large fibre ($12-20\mu$), conducting at velocities above 70 m/sec transmits impulses which reach the extrafusal motor end-plates much more quickly (Hunt 1952; Granit 1957; Brown, et al., 1965), initiating a ballistic response before the gamma system can operate directly on the sensitivity of the spindle. However, fusimotor regulation of the sensitivity or threshold for the firing of the spindle has a powerful indirect influence on the muscle response by biasing the spindle independently of the resting length of the extrafusal fibres (Hammond, et al., 1956; Granit and Henatsch, 1956).

Hence, if alpha and gamma efferent activity occurs concurrently in man, it would be reasonable to expect heightened fusimotor barrage onto the intrafusal motor end-plates of the spindle when the S becomes more activated (Paillard, 1959), and, in these experiments, this would occur when the skin is scratched. Since it is not practicable to record

intrafusal fibre responses directly (except with great difficulty in experimental animals), perhaps the best reliable, indirect estimation of fusimotor activity is the variability of the electrical impulse of the MAP from the responding muscle. In the case of the brief tap (lasting 0.02 sec) to the ligamentum patellae, the resulting volley of centrifugal impulses to the motor end-plates of the extrafusal fibres is highly synchronous. The MAP is a di-phasic or tri-phasic spike which is readily quantifiable in μV secs. This argument is supported by the standard deviation data in Table II. With two exceptions (G.B., Sessions 6 and 7), when the skin is scratched the variability in the MAP becomes greater although, of course, not always significantly and it is most improbable that this increased variance occurred by chance (Sign test; $p < 0.001$). It is known that gamma firing is permanently variable (Granit and Henatsch, 1956) and the observed increase in variability of the MAP could be the reflection of increased fusimotor activity on spindle sensitivity.

Further, support for this hypothesis comes from the knowledge that gamma biasing makes the spindle a much faster and more sensitive organ and therefore an increase in its discharge from the primary ending will occur when the muscle is stretched. This will cause a greater reflex response in the extrafusal fibres and also a decrease in reflex time (Granit and Henatsch 1956; Homma, et al., 1962). Fusimotor biasing of the spindle leads to minute contraction

of the intrafusal fibres and a consequent lowering of the threshold of the primary ending but it does not induce any detectable change in the tension of the extrafusal fibres (Eldred and Fujimori, 1958). These conditions were satisfied in these experiments; that is, there was no significant change in muscle tension between conditions within a session but there was an increase in muscle response and a decrease in latency when the skin over the responding muscle was scratched.

Presumably there are neural pathways from the skin to alpha and gamma motoneurons which are quite specific to the area of skin stimulated. Facilitation is localised to stimulation of the skin over the responding muscle because scratching other skin areas did not produce facilitation. Hence, skin stimulation does not produce a general sensitisation of spindle receptors but rather a particular, reciprocal pattern of muscle facilitation and inhibition.

It may be concluded that both the alpha and gamma motoneurons contribute to the effects of skin stimulation by scratching which have been demonstrated in these experiments using human Ss highly trained in mental and physical relaxation. However, the separate influence of each cannot be determined with any degree of certainty although work in infra-human animal neurophysiology suggests that the fusimotor system has the more active role (Eldred and Hagbarth, 1954).

CHAPTER VII

THE EFFECTS OF VARIOUS TYPES
OF VISUAL AND AUDITORY STIMULI
ON THE PATELLAR REFLEX

The results of experiments dealing with skin stimulation (Chapter VI) revealed that there seemed to be three reliable indices of fusimotor biasing of muscle spindles. These were an increase in amplitude of the reflex, a decrease in reflex latency and an increase in the variance of the responses.

There is evidence in the literature that these measures may be valid indices of fusimotor sensitisation of spindles.

(a) Increased amplitude of the reflex responses

Many reports have appeared in the literature of reflex responses in humans being augmented during arousing conditions such as (a) irrelevant, remote muscle activity (Lombard, 1887; Bowditch and Warren, 1890; Varnum, 1934; Buller and Dornharst, 1957; Paillard, 1959; Rabending and Koch, 1962), (b) mental work (Tuttle, 1924b; Golla and Antonovitch, 1929; Emery, 1931) and (c) a sudden auditory or visual stimulus (Lombard, 1887; Bowditch and Warren, 1890; Lee and Kleitman, 1923; Jacobson and Carlson, 1925). Under these conditions, heightened fusimotor discharge would be expected so that gamma biasing of the muscle spindles would account, in part, for the augmentation of the response (Mark, 1963).

(b) Decreased reflex latency

The inverse relationship between latency and amplitude has been observed by Golla and Hettwer (1923) during 'either physical or psychical effort' and by Varnum (1934) during a Jendrassik manoeuvre. Hence reduced latency is associated with conditions when fusimotor biasing of the spindles would be expected in human subjects.

The decrease in reflex time with concurrent gamma biasing of the intrafusal fibres in infra-human animal experiments has been mentioned previously (Chapter VI).

(c) Increased variance of reflex responses

In reviewing the literature on the patellar reflex, Fearing (1928) has commented that nearly every investigator has noted the enormous variability of the responses. It was shown in Chapter III that this can be attributed to lack of control over relevant variables which affect the response. Without proper control, fusimotor discharge would operate over a large range, biasing the intrafusal fibres in an unpredictable way. There is evidence from experimental neurophysiology to support this view.

Recordings from fusimotor neurones have shown that the intervals between impulses typically are irregular (Hunt and Paintal, 1958). It is not surprising, therefore, to find that the discharge from the primary ending of the spindle is irregular during high fusimotor biasing of the intrafusal fibres

even when the muscle is held at a constant length, whereas, after de-efferentation the spindle response becomes remarkably regular (Granit, 1957; Matthews, 1964). Under normal conditions fusimotor fibres discharge asynchronously (Matthews, 1964) so that increased variance in the reflex would be expected when more fusimotor fibres are activated during arousal states.

In discussing arousal mechanisms Sokolov (1963) has associated supra-spinal centres with variable receptor response by noting that activation of the RF lowers the threshold of the muscle spindle and increases its lability. The 'exacerbation' of the mechanically elicited Achilles reflex during remote muscular action (JM) has been explained by Paillard (1959) by an increase in spindle sensitivity resulting from fusimotor activation. Paillard reached this conclusion because fluctuation of responses to mechanical stimulation occurred when responses to electrical stimulation of afferent nerves gave a narrow distribution of amplitude. Since the H reflex reflects the excitability of the alpha motoneurones only, the observed variance in the mechanically elicited reflex could be attributed to effects emanating from the spindle.

In the present experiments with intact, normal human Ss, it would not be possible to eliminate fusimotor discharge because gamma motoneurones are continually active (Granit, 1957) and, in any event, some degree of intrafusal tone probably is necessary

for the existence of a normal stretch reflex (Eldred, 1960). Therefore, an increase in the variance of responses above control level may be regarded as an index of increased fusimotor activity.

Linearity of the relationship between mechanical and electrical responses

A highly significant, positive, linear relationship was found between the mechanical and electrical responses in the patellar reflex under control conditions when fusimotor activity presumably was reduced to low levels (Chapter V). The consistency of muscle tonus was suggested as one of the main reasons for the high correlation coefficients.

The present experiments provide the opportunity to investigate the effects of marked changes in fusimotor activity on the relationship between the two variables while muscle tonus remains consistent.

Aim of the present experiments

The experiments to be described were designed to

- (i) test the proposition that an increase in amplitude and variance of the responses with a concomitant decrease in latency may be regarded as reliable, indirect indices of increased fusimotor activity, and
- (ii) find out whether strong biasing of the spindle has any effect on the high,

positive correlation coefficients and linearity of the relationship between the mechanical and electrical responses.

Rationale for the experiments

Animal studies

All afferent pathways from sensory receptors make collateral connections with multiple relays in the brain stem (French, et al., 1952; Rossi and Zanchetti, 1957; Magoun, 1958; Lindsley, 1961; Gernandt and Ades, 1964). Hence there is the possibility of accurately controlling the effects of visual and auditory stimuli on the patellar reflex because the activity of the fusimotor system is related to the general level of activation of the RF (Euler and Soderberg, 1957).

The findings from experimental work with animals show that the initial stimulation excites the reticular nuclei and increases the general level of reactivity of the nervous system but repetitive stimulation results in adaptation (Sokolov, 1963).

An experiment which specifically examined the responses of neurones in the RF to natural stimuli was conducted by Bell and associates (Bell, et al., 1964). They studied the parameters of visual, auditory and some other forms of stimuli on single neurones in the mesencephalic RF of anaesthetised cats using micro-pipettes placed stereotaxically. The auditory stimuli used were clicks, claps and

voices while weak light flashes and changes in the room illumination were used as visual stimuli. The results showed that most reticular neurones responded well to the initial presentation of these types of stimuli but with repetitive application of the same stimulus, the frequency and amplitude of reticular activity progressively declined. Maximum arousal was achieved with very few presentations of an intermittent signal but attenuation of reticular activity occurred after about 25 intermittent presentations of the same stimulus. Stimuli were most effective in eliciting responses in reticular units when the frequency of presentation was in the range 0.2 to 10.0 cps (mode about 2 cps).

The presentation of similar types of stimuli to humans may result in parallel characteristics of arousal and attenuation of reticular activity and, consequently, gamma and alpha motoneurone response. A few presentations of stimuli at low frequency (about 2 cps) would allow ample time for the raised supra-spinal excitability to be reflected in spindle biasing by way of the small diameter, slow conducting, fusimotor fibres.

Studies with humans

There is experimental evidence from studies on humans that auditory stimulation in the form of binaurally presented clicks (120 db) evoked a well defined EMG response in arm and leg muscles, the latency in quadriceps being 50 to 60 msec (Bickford,

et al., 1964). However, this response could be demonstrated only when a computer of average transients was used; no signal could be detected in the raw EMG. An interesting associated finding was that the averaged spike was reduced as much as 40 per cent when monaural presentation of the clicks was used. Presumably, either very low voltage MAPs or the discharge of muscle spindles would account for the averaged spike found in the EMG because the recording technique was very sensitive, being capable of detecting any regular signal embedded in background noise provided enough scans are made. In either case, supra-spinal sensitisation of the peripheral mechanisms is indicated because no detectable movement of limbs occurred.

Previous work on the effects of visual and auditory stimuli on the human patellar reflex has been examined (Chapter III) when techniques to attenuate fusimotor discharge were discussed. The survey showed that there has been no systematic investigation of the effects of these stimuli on the reflex response in regard to amplitude, latency and variance.

The present experiments were designed to investigate these aspects of the dependent variables when several types of visual and auditory stimuli were used.

The results will be given separately for each of the four experiments followed by a general discussion.

EXPERIMENT 1

Subjects

Five normal adult Ss (2 males, 3 females), age range 19-24 years, participated in the experiment. All had practised for a minimum of ten separate lh sessions the method of relaxation developed by Jacobson.

Apparatus

As previously described with the following additions.

The room 'house light' was extinguished after the S was connected to the apparatus and light flashes were obtained by using a neon bulb (with a 5 cm x 3.5 cm reflecting plate behind it) powered by a 90 V battery through an appropriate resistor, capacitor and potentiometer circuit to supply flashes at the rate of 2/ sec whenever the circuit was closed by the experimenter (Figure 36, Appendix A). The neon was placed 20 cm directly in front of the S's eyes and provided an illumination of 21.5 lumens/sq metre (equivalent to 2 lumens/sq ft shown in Tables III and IV).

Experimental design

There were three types of experimental sessions:

- (1) 5 control trials when the S was relaxed with eyes open in a blacked-out room

(treatment A); 10 trials as for A but with the experimental treatment of 3 flashes before the pendulum-hammer was released by the E to tap the ligament (treatment B); and finally, treatment A was repeated.

(2) 5 trials under treatment B; 10 control trials under treatment A; and finally, 5 trials under treatment B to test for possible sequential effects of the treatments, and

(3) 5 control trials under treatment A; 10 trials as for A but with the experimental treatment of at least 30 flashes before the tap on the ligament (treatment C); and finally treatment A was repeated.

In all cases the right patellar reflex was investigated isometrically and at least 15 sec were allowed between taps on the ligament. The Ss viewed the light source binocularly.

At the beginning of each session, the force of the tap on the ligament was adjusted so that it was just over the threshold necessary to elicit a brisk reflex.

The predictions were that:

(a) three light flashes should arouse the reticular formation, activate the fusimotor

neurons and thereby bias the muscle spindle. This should result in a significantly increased variance of the MAP from rectus femoris and in an augmented amplitude of responses compared with control responses when the ligamentum patellae is tapped to elicit the reflex, and

- (b) continued presentation of the same visual stimulus for more than 30 flashes should result in attenuation of reticular and fusimotor discharge. Therefore, the variance and the mean amplitude of the responses should not be significantly different from those of control responses.

RESULTS

Data Collection

The independent variable (the maximum force of the tap on the ligamentum patellae) and two dependent variables (the impulse of the MAP from rectus femoris, and the maximum force of the isometric reflex contraction) were observed in the experiment. In addition, latency measures were made in some sessions.

Data were used only if two tailed t -tests for the significance of the difference between means of the force of the tap on the ligament (range of peak force 1.29 to 2.45 kg) under control and experimental treatments showed that no significant difference

existed. Since the pendulum-hammer was released from a constant height within sessions, it could be assumed that no variations, other than those of chance, occurred in muscle tonus between treatments.

One of each of the three types of experimental sessions was obtained for all five Ss. Table III gives data for each of the three types of session with the five Ss.

The effect of 3 light flashes on the dependent variables

There was a significant increase in the variance of the MAP, without exception, across all Ss under this experimental treatment. Four of the Ss also showed a significantly augmented mean MAP impulse whilst the fifth S (L.V.) showed a larger but not significantly increased mean MAP impulse. Similar results were obtained for the maximum force of the isometric contraction because high positive product-moment correlations were obtained within sessions between the two dependent variables (Table III and Figure 15).

Figure 15 also illustrates the increase in mean and variance of the mechanical and electrical responses in treatment B compared with control.

TABLE III

DATA RELEVANT TO THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND THE DEPENDENT VARIABLES (LATENCY, MAXIMUM FORCE OF ISOMETRIC CONTRACTION, AND IMPULSE OF THE MUSCLE ACTION POTENTIAL) DURING CONTROL (A) AND EXPERIMENTAL TREATMENTS OF THREE LIGHT FLASHES (B) AND MORE THAN THIRTY LIGHT FLASHES (C). THE EXPERIMENTS WERE CONDUCTED IN A BLACKED-OUT ROOM AND THE LIGHT FLASHES (ILLUMINATION LEVEL: 2 LUMENS/SQ. FT.; RATE OF PRESENTATION: 2/SEC) WERE VIEWED BINOCULARLY.

| Subject | Sequence | Treatment | Peak Force on Ligament (kg) | | Latency (msec) | | | Maximum Force of Isometric Contraction (kg) | | | | Impulse of M.A.P. (μ V sec) | | | | Correlation Max. Force & M.A.P. | N | | |
|---------|----------|-----------|-----------------------------|------|----------------|--------|----|---|---------|----------------|---------|----------------------------------|---|----------------|---------|---------------------------------|---------|-------|----|
| | | | \bar{X} | t | \bar{X} | t | df | \bar{X} | t | S ² | F | \bar{X} | t | S ² | F | | | | |
| R.R. | ABA | Control | 1.43 | | Not available* | | | 0.48 | | 0.04 | | | | 1.67 | | 0.48 | | 0.987 | 10 |
| | | Exper. | 1.42 | 0.41 | | | | 1.98 | 5.51*** | 0.71 | 20.2*** | | | 5.74 | 5.81*** | 4.84 | 9.99** | 0.929 | 10 |
| | ACA | Control | 1.64 | | Not available | | | 0.88 | | 0.25 | | | | 2.62 | | 1.78 | | 0.964 | 10 |
| | | Exper. | 1.62 | 0.75 | | | | 0.56 | 1.81 | 0.12 | 1.94 | | | 1.76 | 1.60 | 1.13 | 1.57 | 0.958 | 10 |
| | BAB | Control | 1.51 | | 20.6 | 2.15* | 17 | 0.56 | | 0.15 | | | | 1.62 | | 1.25 | | 0.998 | 10 |
| | | Exper. | 1.53 | 0.66 | 18.3 | | | 1.65 | 3.95*** | 0.49 | 3.21* | | | 5.36 | 4.22*** | 6.59 | 5.27* | 0.959 | 10 |
| W.R. | ABA | Control | 2.15 | | Not available | | | 0.31 | | 0.02 | | | | 0.87 | | 0.03 | | 0.651 | 10 |
| | | Exper. | 2.16 | 0.49 | | | | 0.54 | 3.37** | 0.03 | 1.69 | | | 1.16 | 2.19* | 1.15 | 4.44* | 0.738 | 10 |
| | ACA | Control | 2.11 | | Not available | | | 0.29 | | 0.04 | | | | 0.64 | | 0.17 | | 0.883 | 10 |
| | | Exper. | 2.11 | 0.00 | | | | 0.11 | 2.57* | 0.01 | 5.18* | | | 0.38 | 1.38 | 0.19 | 1.16 | 0.942 | 10 |
| | BAB | Control | 1.92 | | Not available | | | 0.23 | | 0.07 | | | | 0.51 | | 0.15 | | 0.965 | 10 |
| | | Exper. | 1.91 | 0.50 | | | | 0.55 | 1.74 | 0.26 | 3.59* | | | 1.49 | 2.39* | 1.51 | 9.91*** | 0.931 | 10 |
| B.H. | ABA | Control | 1.44 | | Not available | | | 0.83 | | 0.08 | | | | 1.05 | | 0.28 | | 0.896 | 10 |
| | | Exper. | 1.44 | 0.00 | | | | 1.50 | 3.19** | 0.37 | 4.49* | | | 2.37 | 3.28** | 1.34 | 4.82* | 0.993 | 10 |
| | ACA | Control | 1.53 | | Not available | | | 0.66 | | 0.18 | | | | 1.35 | | 1.11 | | 0.994 | 10 |
| | | Exper. | 1.54 | 0.49 | | | | 0.33 | 2.28* | 0.03 | 5.10* | | | 0.68 | 1.88 | 0.18 | 6.24** | 0.993 | 10 |
| | BAB | Control | 1.35 | | 20.4 | | | 0.49 | | 0.09 | | | | 2.09 | | 1.49 | | 0.989 | 10 |
| | | Exper. | 1.37 | 0.66 | 19.5 | 3.57** | 12 | 1.13 | 2.93** | 0.38 | 4.18* | | | 5.48 | 3.48** | 7.99 | 5.36** | 0.989 | 10 |
| L.V. | ABA | Control | 1.90 | | Not available | | | 0.63 | | 0.08 | | | | 0.29 | | 0.03 | | 0.952 | 10 |
| | | Exper. | 1.91 | 0.42 | | | | 0.93 | 1.78 | 0.22 | 2.84 | | | 0.48 | 1.49 | 0.12 | 4.24* | 0.932 | 10 |
| | ACA | Control | 2.12 | | Not available | | | 0.62 | | 0.09 | | | | 0.39 | | 0.06 | | 0.969 | 10 |
| | | Exper. | 2.12 | 0.00 | | | | 0.53 | 0.77 | 0.04 | 2.14 | | | 0.33 | 0.19 | 0.04 | 1.39 | 0.870 | 10 |
| | BAB | Control | 2.39 | | Not available | | | 0.49 | | 0.02 | | | | 1.23 | | 0.09 | | 0.881 | 10 |
| | | Exper. | 2.39 | 0.00 | | | | 0.70 | 0.88 | 0.56 | 32.9*** | | | 1.69 | 0.83 | 3.13 | 34.1*** | 0.999 | 10 |
| M.D. | ABA | Control | 1.97 | | Not available | | | 0.71 | | 0.07 | | | | 0.21 | | 0.04 | | 0.949 | 10 |
| | | Exper. | 1.96 | 0.29 | | | | 1.49 | 3.01** | 0.59 | 8.12** | | | 0.67 | 2.10* | 0.47 | 11.1*** | 0.937 | 10 |
| | ACA | Control | 1.91 | | Not available | | | 0.44 | | 0.09 | | | | 0.92 | | 0.38 | | 0.848 | 10 |
| | | Exper. | 1.95 | 1.76 | | | | 0.50 | 0.44 | 0.12 | 1.28 | | | 0.99 | 0.23 | 0.55 | 1.43 | 0.986 | 10 |
| | BAB | Control | 1.86 | | 21.2 | | | 0.66 | | 0.13 | | | | 0.42 | | 0.06 | | 0.970 | 10 |
| | | Exper. | 1.83 | 1.05 | 20.6 | 2.27* | 10 | 1.31 | 2.79* | 0.42 | 3.15* | | | 0.99 | 2.67* | 0.42 | 7.68** | 0.957 | 10 |

Probability levels: *P < 0.05, **P < 0.01, ***P < 0.001

*These data were not available unless an assistant was present because the experiments were conducted in a blacked-out room.

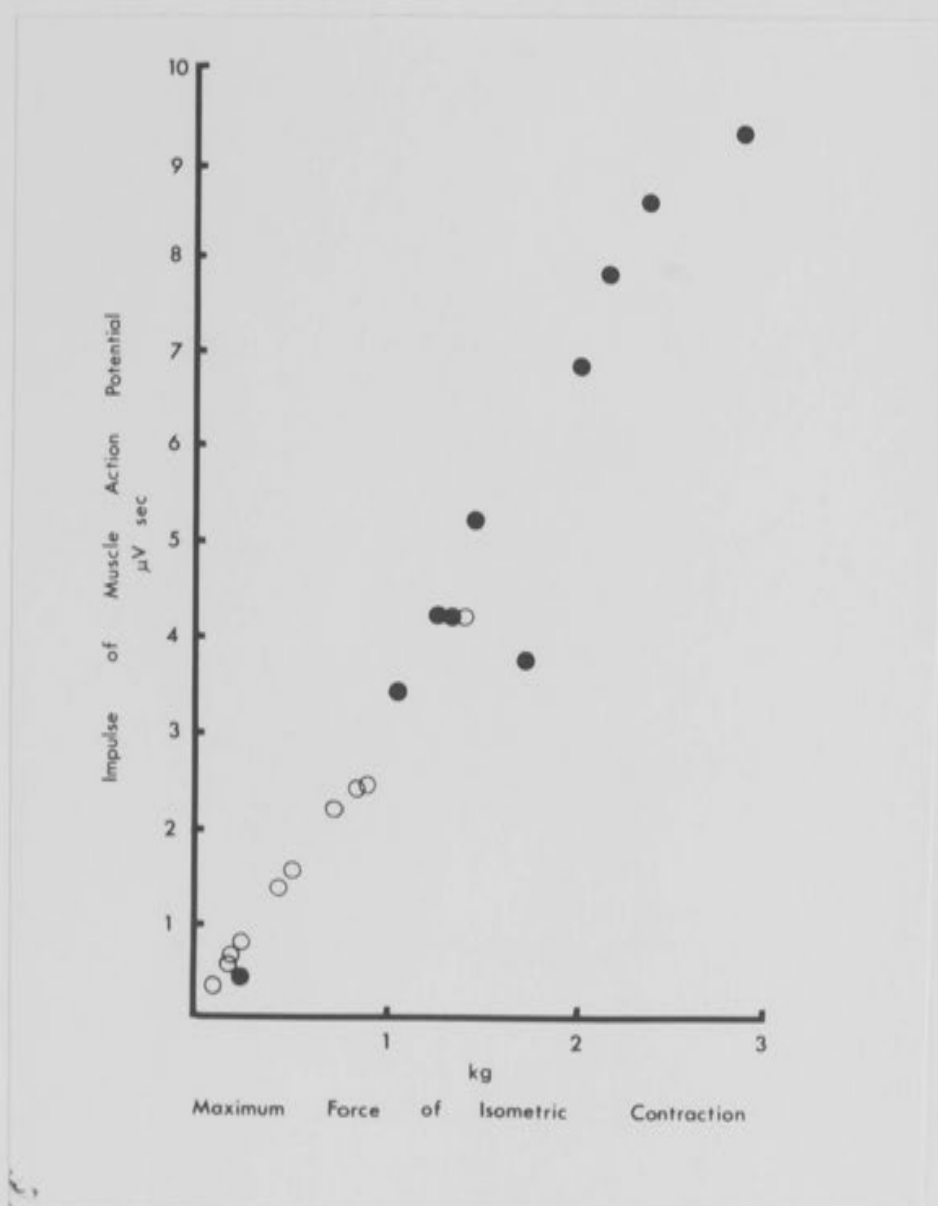


Figure 15

Graph to show the high, positive relationship between the electrical and mechanical responses of the patellar reflex under treatment A ($r = 0.998$) and treatment B ($r = 0.959$). The increase in variance and mean amplitude of the responses under treatment B (3 light flashes) compared with treatment A (Control) is evident. o treatment A; ● treatment B. Subject R.R.

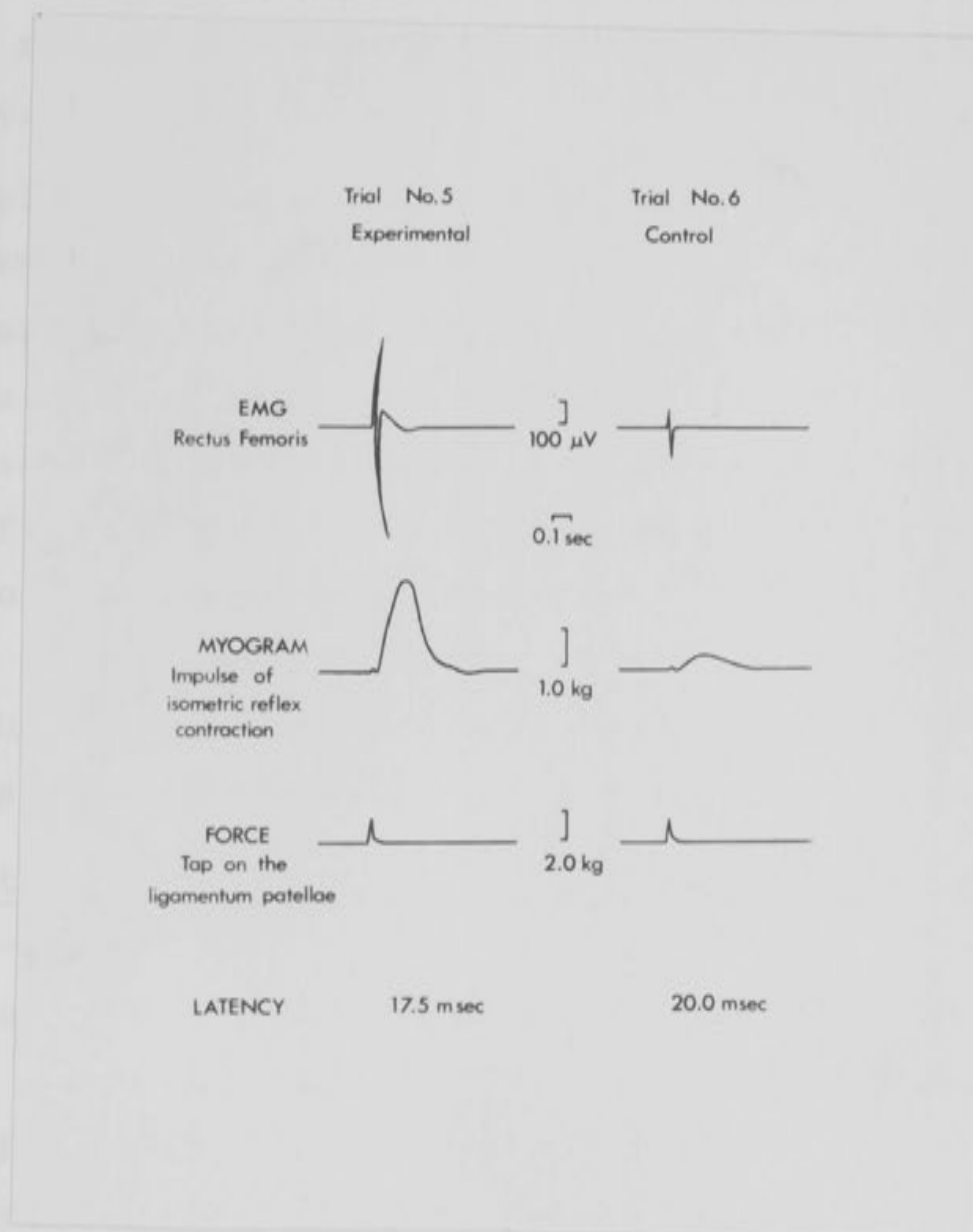


Figure 16

The records of two successive trials to show changes in the EMG, myogram and latency which occurred between treatments B (left) and A (right). Subject B.H.

In general, the visual stimulus of 3 light flashes increased the variance and amplitude of responses compared with control responses. Figure 16 shows two successive trials (subject B.H.) to illustrate the change in response between experimental and control treatments.

Correlation coefficients between the maximum force of the isometric contraction and the impulse of the MAP were similar for control and experimental treatments. Even when the data for the 20 trials within a session were pooled, the coefficient was not significantly different from the coefficients for each of the separate treatments (Table III). Figure 15 shows the linearity of the relationship between the mechanical and electrical responses during the two treatments.

The effect of more than 30 light flashes on the dependent variables

For only one S did this experimental treatment result in a significant difference in the variance of the MAP compared with control and the exception was a decrease in variance. Without exception across Ss there was no difference in mean impulse of the MAP between control and experimental treatments. The trend was a reduction in variance and mean amplitude of both dependent variables during treatment C (Table III and Figure 17) and for two Ss (B.H. and W.R.) these statistics were significant for the maximum force of the isometric response.

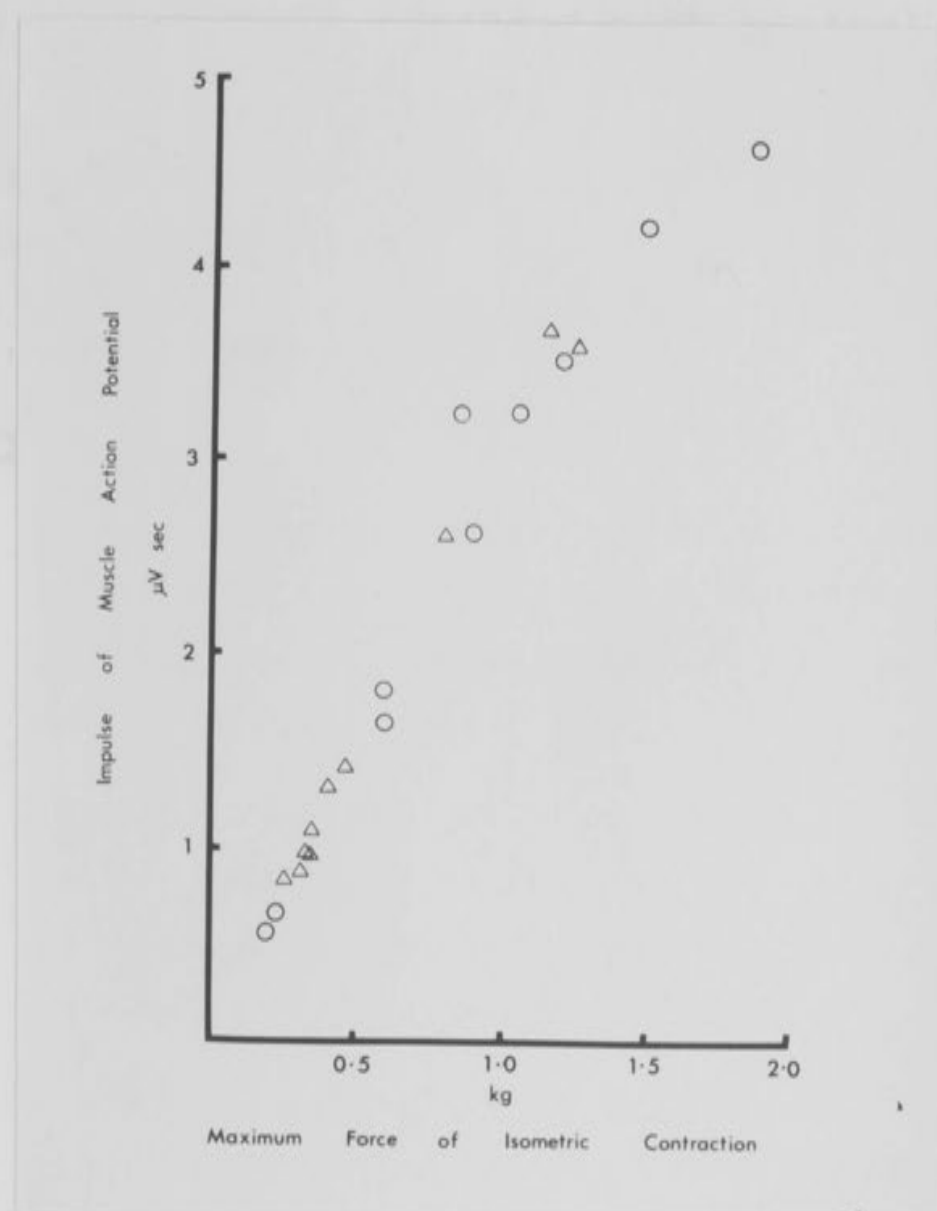


Figure 17

Graph to show the relationship between the electrical and mechanical responses of the patellar reflex under treatment C (30 light flashes) and treatment A (Control). $r_a = 0.964$, $r_c = 0.958$. The slight, but non-significant, decrease in variance and mean amplitude of the responses during the experimental treatment is evident. o treatment A; Δ treatment C. Subject R.R.

In general, the presentation of 30 flashes of light had no significant effect on the variance and amplitude of responses compared with control responses.

The high, positive correlation coefficients between the mechanical and electrical responses were preserved under treatment C (Table III and Figure 17).

Subsidiary results

- (a) Latency was recorded in three sessions (Table III). The mean reflex time was shorter during treatment B than during control conditions.
- (b) Results for all Ss were independent of the sequence in which the treatment was presented. Results were similar whether an ABA or BAB design was used (Table III).
- (c) Some experiments were conducted to discover what changes in the force of the tap on the ligament were necessary to elicit a mean impulse of the MAP during
 - (i) treatment B which was not significantly different from treatment A, and
 - (ii) treatment A which was not significantly different from treatment B.

Table IIIa gives data for subject R.R. and indicates that changes of over 20 per cent were required in the

TABLE IIIa

Data to show the changes in force of tap on the ligamentum patellae to achieve certain criterion MAP responses

| Mean peak force of tap on ligament (kg) | Experimental Condition | Two tailed <u>t</u> -test for significance of difference between mean MAP impulse | Degrees of Freedom | P |
|---|---|---|--------------------|----------|
| 1.72 | Treatment D (Treatment A but increased force on ligament) | } 0.17 | 8 | Not Sig. |
| 1.42 | Treatment B | | | |
| 1.39 | Treatment A | } 3.66 | 8 | < 0.01 |
| 0.99 | Treatment E (Treatment B but reduced force on ligament) | } 0.30 | 8 | Not Sig. |

There is a significant difference in mean impulse of the MAP between treatments A and B but not between treatments B and D, and treatments A and E. Subject R.R.

force applied to the ligament to achieve the criterion MAP responses. In absolute units, the minimum change in force was 298 g.

EXPERIMENT 2

Subjects

Three Ss (1 male, 2 females) participated in this experiment involving monocular presentation of the visual stimuli.

Apparatus

As in experiment 1.

Experimental design

The light flashes were presented in the same way as before except that the S had one eye covered with an opaque shield for monocular trials.

It was necessary to investigate binocular and both types of monocular presentation within each session so that all treatments could be compared during otherwise similar organismic conditions.

Since about 30 trials are the maximum during which a S can hold a reasonably consistent level of relaxation, these sessions consisted of 10 control, 10 binocular and 5 of each type of monocular presentation except in session 2, R.R., where there were 10 trials for each monocular treatment.

In the light of Bickford's findings (1964), it was predicted that there would be a reduction in the mean and variance obtained with monocular presentation compared with binocular presentation.

RESULTS

Data collection

There was no significant difference in the mean peak force of the tap on the ligament between treatments.

The impulse of the MAP was used as the dependent variable.

The effect of ipsilateral visual stimulation

Without exception, no significant difference was found between the means and variances of the impulse of the MAP for the three Ss during monocular trials even though these statistics were significant during binocular trials in the same session (Table IV).

The effect of contralateral visual stimulation

The mean and variance of the MAP were larger during the experimental treatment than during control treatment but, generally, these statistics were not significant (Table IV).

TABLE IV

DATA TO SHOW THE COMPARISON BETWEEN THE EFFECTS OF BINOCULAR AND TWO TYPES OF MONOCULAR PRESENTATION OF VISUAL STIMULI ON THE IMPULSE OF THE MUSCLE ACTION POTENTIAL FROM RECTUS FEMORIS (RIGHT LIMB) DURING THE ISOMETRIC REFLEX RESPONSE. EXPERIMENTAL TREATMENT: 3 FLASHES OF LIGHT PRESENTED AT THE RATE OF 2/SEC AND AT AN ILLUMINATION LEVEL OF 2 LUMENS/SQ.FT.

| Subject | Session | Treatment | IMPULSE OF MUSCLE ACTION POTENTIAL FROM RECTUS FEMORIS (RIGHT LIMB) | | | | | | | | | | | | | | |
|---------|---------|-----------|---|-----------|--------|----------------|--------|--|-----------|------|----------------|------|--|-----------|--------|----------------|-------|
| | | | BINOCULAR PRESENTATION | | | | | MONOCULAR PRESENTATION ($\mu\text{V sec}$) Stimulus to right eye | | | | | MONOCULAR PRESENTATION Stimulus to left eye | | | | |
| | | | N | \bar{X} | t | S ² | F | N | \bar{X} | t | S ² | F | N | \bar{X} | t | S ² | F |
| B.H. | 1 | Control | 10 | 2.85 | | 2.39 | | 10 | 2.85 | | 2.39 | | 10 | 2.85 | | 2.39 | |
| | | Exper. | 10 | 6.89 | 3.29** | 12.6 | 5.28* | 5 | 3.00 | 0.15 | 6.68 | 2.78 | 5 | 5.56 | 3.24** | 14.9 | 6.22* |
| | 2 | Control | 10 | 2.09 | | 1.49 | | 10 | 2.09 | | 1.49 | | 10 | 2.09 | | 1.49 | |
| | | Exper. | 10 | 5.48 | 3.48** | 7.99 | 5.36** | 5 | 3.38 | 2.09 | 0.67 | 2.24 | 5 | 3.79 | 1.84 | 6.41 | 4.30 |
| R.R. | 1 | Control | 5 | 2.06 | | 1.57 | | 5 | 2.06 | | 1.57 | | 5 | 2.06 | | 1.57 | |
| | | Exper. | 5 | 5.65 | 3.66** | 3.26 | 2.09 | 5 | 2.81 | 0.81 | 2.75 | 1.76 | 5 | 3.87 | 1.77 | 3.66 | 2.33 |
| | 2 | Control | 10 | 2.16 | | 1.84 | | 10 | 2.16 | | 1.84 | | 10 | 2.16 | | 1.84 | |
| | | Exper. | 10 | 5.14 | 3.29** | 6.41 | 3.48* | 5 | 2.22 | 0.93 | 0.49 | 3.78 | 10 | 3.50 | 1.78 | 3.83 | 2.08 |
| M.D. | 1 | Control | 10 | 0.42 | | 0.06 | | 10 | 0.42 | | 0.06 | | 10 | 0.42 | | 0.06 | |
| | | Exper. | 10 | 0.99 | 2.67* | 0.42 | 7.68** | 5 | 0.31 | 0.86 | 0.08 | 1.46 | 5 | 0.50 | 0.14 | 0.36 | 6.49* |

Probability levels: *P < 0.05, **P < 0.01

EXPERIMENT 3

Subjects

Five Ss (3 males, 2 females) participated in this experiment.

Apparatus

As in experiment 1, except instead of a visual stimulus, an auditory stimulus was delivered to headphones from an audio-oscillator which could be turned on and off by the E.

Experimental design

There were two types of experimental sessions:

- (a) 5 control trials with the S relaxed and the eyes masked (treatment A); 10 experimental trials consisting of a random mixture of 5 trials when a tone (1000 cps; 75 db, C scale, Dawe 1400E, S.L.M.) was presented for 5 seconds and the tap was delivered within 1 second of its cessation, and 5 trials when the tap was delivered 1 second after the tone began (treatment S); and finally, treatment A was repeated,
- (b) the treatments were presented in the order SAS to test for possible sequential effects.

The random presentation of the two types of trials in treatment S was adopted to prevent conditioning occurring to the tone.

It was expected that the experimental treatment of a sudden change in sound level would augment the response, reduce the latency and increase the variance of the reflex.

RESULTS

Data collection

There was no significant difference in the mean peak force of the tap on the ligament between treatments (Table V).

The dependent variables observed were latency, maximum force of the isometric contraction and impulse of the MAP.

Latency

There was no significant difference in latency between control and experimental treatments for any S (Table V).

Maximum force of isometric contraction

There was no consistent trend in the differences between means for this variable. In 5 of the 14 sessions the variance increased significantly during the experimental treatment (Table V).

TABLE V
 DATA RELEVANT TO THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND THE DEPENDENT VARIABLES
 (LATENCY, MAXIMUM FORCE OF ISOMETRIC CONTRACTION, AND IMPULSE OF THE MUSCLE ACTION POTENTIAL) DURING CONTROL (A) AND
 EXPERIMENTAL TREATMENT OF A CHANGE IN SOUND LEVEL 1 SEC BEFORE THE TAP ON THE LIGAMENT.

| Subject | Sequence | Treatment | Peak Force on Ligament (kg) | | Latency (msec) | | | Maximum Force of Isometric Contraction (kg) | | | | Impulse of M.A.P. (µV sec) | | | | Correlation Max. Force and M.A.P. | | Z test for difference between correlation coefficients | t test for difference between slopes of regression lines |
|---------|----------|-----------|-----------------------------|---------------|----------------|------|------|---|-------|----------------|---------|----------------------------|------|----------------|----------------|-----------------------------------|----------|--|--|
| | | | \bar{X} | t | \bar{X} | t | df | \bar{X} | t | S ² | F | \bar{X} | t | S ² | F | r | N | | |
| G.B. | ASA | Control | 2.27 | 0.00 | 18.4 | 0.27 | 18 | 1.18 | 0.92 | 0.17 | 1.83 | 3.49 | 0.71 | 1.01 | 1.38 | 0.858 | 10 | 0.80 | - |
| | | Exper. | 2.27 | | 18.5 | | | 1.01 | 0.92 | 0.15 | | 3.15 | | 1.39 | | 0.936 0.896 | 10 20 | | |
| | ASA | Control | 2.00 | 0.34 | 19.7 | 1.73 | 10 | 1.08 | 0.46 | 0.19 | 4.83* | 1.18 | 0.79 | 0.42 | 6.25** | 0.795 | 10 | 0.96 | 0.65 |
| | | Exper. | 2.01 | | 19.4 | | | 1.00 | 0.46 | 0.04 | | 1.06 | | 0.07 | | 0.923 0.819 | 10 20 | | |
| | ASA | Control | 1.67 | 1.42 | 20.2 | 0.70 | 18 | 1.03 | 2.07 | 0.02 | 41.3*** | 0.66 | 1.99 | 0.02 | 11.8*** | 0.928 | 10 | 0.67 | 0.47 |
| Exper. | | 1.75 | | 20.1 | | | 1.65 | 2.07 | 0.89 | | 1.63 | | 2.36 | | 0.964 0.967 | 10 20 | | | |
| SAS | Control | 1.60 | 0.81 | 18.5 | 1.00 | 5 | 1.55 | 0.08 | 0.07 | 6.20** | 3.51 | 0.17 | 0.63 | 4.97* | 0.969 | 10 | 0.75 | - | |
| | Exper. | 1.63 | | 19.1 | | | 1.56 | 0.08 | 0.40 | | 3.62 | | 3.11 | | 0.986 0.908 | 10 20 | | | |
| SAS | Control | 2.12 | 0.21 | 17.9 | 1.01 | 18 | 2.03 | 0.16 | 0.06 | 6.83** | 1.68 | 0.53 | 0.17 | 4.16* | 0.938 | 10 | 1.35 | - | |
| | Exper. | 2.11 | | 18.3 | | | 2.06 | 0.16 | 0.41 | | 1.83 | | 0.69 | | 0.985 0.970 | 10 20 | | | |
| A.N. | ASA | Control | 1.77 | 1.64 | not available | | | 1.17 | 1.98 | 0.29 | 3.05 | 0.49 | 1.93 | 0.16 | 7.09** | 0.949 | 10 | 0.04 | 1.76 |
| | | Exper. | 1.73 | | | | | 0.78 | 1.98 | 0.09 | | 0.23 | | 0.02 | | 0.951 0.946 | 10 20 | | |
| ASA | Control | 2.10 | 0.95 | 19.7 | 1.59 | 16 | 1.04 | 1.01 | 0.14 | 1.12 | 0.46 | 0.97 | 0.05 | 1.37 | 0.941 | 10 | 1.15 | 0.03 | |
| | Exper. | 2.12 | | 19.6 | | | 1.21 | 1.01 | 0.16 | | 0.55 | | 0.04 | | 0.836 0.866 | 10 20 | | | |
| W.B. | ASA | Control | 2.80 | 0.25 | not available | | | 0.24 | 2.34* | 0.03 | 5.84** | 0.29 | 2.19 | 0.05 | 5.53** | 0.960 | 10 | 0.04 | 0.22 |
| | | Exper. | 2.79 | | | | | 0.56 | 2.34* | 0.16 | | 0.68 | | 0.25 | | 0.964 0.969 | 10 20 | | |
| | ASA | Control | 2.08 | 0.67 | 23.6 | 1.63 | 5 | 0.35 | 1.79 | 0.04 | 1.94 | 0.71 | 1.38 | 0.11 | 1.45 | 0.969 | 10 | 1.13 | - |
| Exper. | 2.09 | | 23.3 | | | 0.21 | 1.79 | 0.02 | | 0.52 | | 0.07 | | 0.895 0.942 | 10 20 | | | | |
| ASA | Control | 2.56 | 1.48 | not available | | | 0.24 | 1.65 | 0.04 | 1.62 | 0.48 | 1.39 | 0.11 | 1.97 | 0.961 | 10 | 0.50 | - | |
| | Exper. | 2.52 | | | | | 0.41 | 1.65 | 0.06 | | 0.74 | | 0.22 | | 0.934 0.946 | 10 20 | | | |
| B.H. | ASA | Control | 1.66 | 2.02 | 19.7 | 0.27 | 14 | 0.59 | 2.55* | 0.06 | 2.14 | 0.96 | 1.93 | 0.25 | 3.14 | 0.983 | 10 | 1.21 | 1.22 |
| | | Exper. | 1.62 | | 19.6 | | | 0.34 | 2.55* | 0.03 | | 0.61 | | 0.08 | | 0.939 0.973 | 10 20 | | |
| SAS | Control | 1.95 | 0.89 | 19.9 | 0.96 | 18 | 0.39 | 0.99 | 0.04 | 5.97** | 1.19 | 1.31 | 0.26 | 5.08* | 0.975 | 10 | 0.39 | - | |
| | Exper. | 1.97 | | 19.8 | | | 0.55 | 0.99 | 0.21 | | 1.72 | | 1.33 | | 0.962 0.958 | 10 20 | | | |
| L.V. | ASA | Control | 2.19 | 0.92 | 18.3 | 1.11 | 15 | 1.12 | 0.95 | 0.08 | 1.35 | 1.71 | 0.47 | 0.87 | 7.89** | 0.890 | 10 | 1.35 | - |
| | | Exper. | 2.21 | | 18.8 | | | 0.99 | 0.95 | 0.10 | | 1.57 | | 0.11 | | 0.973 0.885 | 10 20 | | |
| ASA | Control | 1.97 | 0.00 | 18.5 | 0.00 | 12 | 0.89 | 2.06 | 0.08 | 2.83 | 0.84 | 1.78 | 0.10 | 5.85* | 0.934 | 10 | 0.85 | 1.72 | |
| | Exper. | 1.97 | | 18.5 | | | 1.25 | 2.06 | 0.23 | | 1.31 | | 0.59 | | 0.973 0.971 | 10 20 | | | |

Probability levels: *P < 0.05, **P < 0.01, ***P < 0.001

Impulse of the MAP

In no session did the difference between the means show significance (Table V).

Six of the F ratio tests showed that the variance increased significantly during the experimental treatment but this result is not different from chance (Sign test, $p < 0.29$). In fact, on two other occasions (G.B. session 2, and L.V. session 1) there was a reduction in variance.

Correlation coefficients

High, positive product-moment correlations were obtained between the mechanical and electrical responses whether the sets of observations for control and experimental treatments were taken separately or together. Z tests for the difference between correlation coefficients (control and experimental treatments) were not significant. A number of t-tests for the difference between the slopes of the regression lines were conducted and in no instance did these show significance (Table V).

EXPERIMENT 4

Subjects

Three subjects (1 male, 2 females) participated in the experiment.

Apparatus

As in experiment 1 except that auditory stimulation was used instead of visual.

The auditory stimulus was obtained by using an appropriate resistor, capacitor and potentiometer circuit powered with a 90 V battery (Figure 36, Appendix A). Clicks from this circuit were delivered at the rate of 2/sec at a sound level of 70 db (C scale, Dawe 1400E, S.L.M.) to a pair of headphones.

Experimental design

There were three types of experimental sessions similar to those described in experiment 1 but clicks were presented instead of light flashes. The 10 trials with 3 clicks were designated treatment H and the 10 trials with 30 clicks were designated treatment J.

The predictions were the same as in experiment 1.

RESULTS

Data collection

The same independent and dependent variables were observed as those in experiment 1. The product-moment correlations between mechanical and electrical responses were calculated.

No significant difference existed between the means of the peak force on the ligament between treatments within a session.

Table VI gives the data for each of the three types of session with the five Ss.

The effect of 3 clicks on the dependent variables

Without exception the Ss increased the mean of the mechanical and electrical responses during treatment H (3 clicks) compared with treatment A (control).

The variance ratios were significant for the MAP impulse in every session where treatment H was used and although only a half of these ratios were significant for the maximum force of the isometric contraction, all were in the predicted direction (Table VI).

A significant reduction in latency was observed in 50 per cent of occasions. However, all but one of the comparisons with control showed a reduction in reflex time.

High, positive correlation coefficients were found during control and experimental treatments (Table VI).

The effect of more than 30 clicks on the dependent variables

In no instance was there an increase in mean or variance of the mechanical and electrical responses during treatment J; in fact, two of the Ss showed a significant reduction in mean response compared with treatment A (Control). Table VI.

TABLE VI
 DATA RELEVANT TO THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND THE
 DEPENDENT VARIABLES (LATENCY, MAXIMUM FORCE OF ISOMETRIC CONTRACTION AND IMPULSE OF THE MUSCLE ACTION
 POTENTIAL) DURING CONTROL (A) AND EXPERIMENTAL TREATMENTS OF 3 CLICKS (H) AND MORE THAN 30 CLICKS (J).
 THE CLICKS WERE PRESENTED BINAURALLY AT THE RATE OF 2/SEC. AT A SOUND LEVEL OF 70 db.

| Subject | Sequence | Treatment | Peak Force on Ligament (kg) | | Latency (msec) | | | Maximum Force of Isometric Contraction (kg) | | | | Impulse of M.A.P. (μ V sec) | | | | Correlation Max. Force and M.A.P. | N |
|---------|----------|-----------|-----------------------------|------|----------------|---------|----|---|---------|----------------|---------|----------------------------------|---------|----------------|--------|-----------------------------------|----|
| | | | \bar{X} | t | \bar{X} | t | df | \bar{X} | t | S ² | F | \bar{X} | t | S ² | F | | |
| R.R. | AHA | Control | 1.25 | 1.96 | 18.2 | 0.38 | 16 | 1.93 | 3.39* | 0.29 | 2.23 | 2.42 | 2.38* | 0.57 | 3.38* | 0.945 | 10 |
| | | Exper. | 1.30 | | 18.5 | | | 2.97 | | 0.65 | | 3.61 | | 1.92 | | 0.944 | 10 |
| | AJA | Control | 1.30 | 0.99 | 19.1 | 0.33 | 7 | 1.83 | 2.28* | 0.67 | 1.13 | 4.32 | 2.09 | 7.62 | 1.56 | 0.904 | 10 |
| | | Exper. | 1.32 | | 19.5 | | | 1.02 | | 0.59 | | 1.89 | | 4.88 | | 0.908 | 10 |
| | HAH | Control | 1.09 | 0.90 | 20.8 | 1.23 | 10 | 0.52 | 3.91** | 0.25 | 1.97 | 0.84 | 3.47** | 0.75 | 4.47* | 0.968 | 10 |
| | | Exper. | 1.13 | | 19.6 | | | 1.59 | | 0.50 | | 3.06 | | 3.35 | | 0.870 | 10 |
| B.H. | AHA | Control | 1.59 | 1.41 | 21.2 | 2.43* | 17 | 0.54 | 2.33* | 0.08 | 6.44** | 2.12 | 2.27* | 1.48 | 5.74** | 0.947 | 10 |
| | | Exper. | 1.60 | | 20.2 | | | 1.09 | | 0.49 | | 4.48 | | 8.47 | | 0.964 | 10 |
| | AJA | Control | 0.89 | 0.14 | 19.9 | 0.88 | 17 | 0.66 | 0.52 | 0.13 | 2.48 | 2.79 | 1.05 | 1.82 | 1.87 | 0.992 | 10 |
| | | Exper. | 0.90 | | 20.2 | | | 0.55 | | 0.32 | | 2.04 | | 3.41 | | 0.962 | 10 |
| | HAH | Control | 1.58 | 0.81 | 20.8 | 3.83** | 17 | 0.34 | 4.23*** | 0.04 | 17.6*** | 1.06 | 4.99*** | 0.55 | 5.54** | 0.993 | 10 |
| | | Exper. | 1.61 | | 19.2 | | | 1.44 | | 0.64 | | 4.07 | | 3.09 | | 0.945 | 10 |
| M.D. | AHA | Control | 1.24 | 1.28 | 22.0 | 4.46*** | 15 | 0.56 | 6.76*** | 0.22 | 3.48* | 1.44 | 4.48*** | 1.37 | 7.01** | 0.966 | 10 |
| | | Exper. | 1.21 | | 20.1 | | | 2.67 | | 0.75 | | 6.54 | | 9.61 | | 0.866 | 10 |
| | AJA | Control | 1.34 | 0.60 | 21.3 | 2.36* | 14 | 1.02 | 2.67* | 0.31 | 1.27 | 2.39 | 3.02** | 1.66 | 2.32 | 0.922 | 10 |
| | | Exper. | 1.35 | | 22.3 | | | 0.44 | | 0.16 | | 0.93 | | 0.71 | | 0.962 | 10 |
| | HAH | Control | 1.64 | 0.27 | 21.3 | 1.85 | 11 | 0.42 | 6.13*** | 0.24 | 2.30 | 0.79 | 4.63*** | 0.69 | 14.1** | 0.994 | 10 |
| | | Exper. | 1.65 | | 20.1 | | | 2.16 | | 0.56 | | 5.52 | | 9.69 | | 0.973 | 10 |

Probability levels: *p<0.05, **p<0.01, ***p<0.001

In every case there was an increase in mean latency although only one S (M.D.) showed a significant increase (Table VI).

Correlation coefficients were not adversely affected by treatment J compared with coefficients obtained during treatment A.

DISCUSSION

The results of these four experiments dealing with the effects of visual and auditory stimuli on the patellar reflex will be discussed collectively.

Augmentation

The results from experiments 1 and 4 show that when a brief train of (a) visual stimuli are presented binocularly or (b) auditory stimuli are presented binaurally, there is an increase of activity in the alpha motoneurons to the rectus femoris muscle in a phasic stretch reflex.

The results from experiment 3, however, show that a single change in sound level (that is, from silence to a maintained tone of 1000 cps at 75 db or from the tone maintained for 5 sec to silence) just before the tap on the ligament, is insufficient to augment the response.

Gernandt and Ades (1964) found that a supra-maximal click stimulus (7.5 cps, greater than 137 db) was necessary to send well synchronised impulses to the brain stem of cats with the left cochlea removed.

Despite this monaural reception of the click stimuli, large responses were recorded bilaterally through both the medial and lateral RF, apparently because functional crossings occur in the brain stem. This activity in the RF initiated a pattern of descending impulses in the spinal cord. White noise of high intensity failed to elicit these reactions. Apparently, a well synchronised stimulus such as a click or a flash is necessary to arouse the RF sufficiently to activate descending pathways in the spinal cord. If this is the case, then the single change of sound level in experiment 3 was not intense enough (75 db) or of sufficient contrast (1000 cps) to synchronise the input to the RF and arouse descending pathways.

The possibility that the results obtained may be due to changes in the rate and amount of extension of the ligament, brought about by alterations in muscle tone, must be considered. However the pendulum-hammer was released from a uniform height within sessions and observations of the force of the tap on the ligament showed that no significant change in mean force occurred between treatments (Tables III, V, VI). Therefore, muscle tonus remained quite consistent and changes which were observed in the dependent variables between treatments must be attributed to other sources.

In no instance was there evidence in the experimental trials of conditioned or anticipatory responses occurring prior to the tap on the ligament.

There was no gradual increase in the amplitude of responses as a function of the number of trials as would be expected if conditioning had occurred to the light stimulus; nor was there any evidence whatsoever of anticipatory responding which would be shown by deflection of the electromyogram and the myogram prior to the tap on the ligament. In addition, when the 3 light flashes were presented monocularly to the ipsilateral eye, the effects obtained during binocular presentation were lost (Table IV). Hence, it is most unlikely that the results can be explained in terms of specific cortical learning and an explanation must be sought in mechanisms at lower levels of the CNS involving a more general arousal system. The effects obtained appear to be the result of influences descending from reticular levels of the CNS. These probably were a combination of indirect influence (fusimotor biasing of spindle sensitivity) and direct influence (centrifugal sensitisation of alpha motoneurones) because both systems appear to be co-excited by descending impulses (Granit, et al., 1959). The separate effects of these two factors cannot be assessed in these experiments. However, direct facilitation of alpha motoneurones probably plays an active role by adding a fairly constant augmentation under the conditions of relaxation in the present experiments. Magladery, Teasdall, Park and Porter (1951) and Landau and Clare (1964) have shown that H reflexes of fairly constant amplitude could be obtained provided the S was relaxed.

Paillard (Figures 1 and 6, 1959) has shown results which indicate that similar consistency of the H reflex could be achieved even when a JM was used concurrently.

Figure 16 shows that the MAP differed in amplitude under experimental and control treatments but remained di-phasic. This feature was observed generally and indicates a recruitment of alpha motor units in treatment B presumably because of the lowered threshold of the spindles. The changes in force on the ligament of at least 20 per cent (Table IIIa) which are required to match certain criterion responses, indicate the strong effects of a briefly presented train of intermittent visual stimuli on the threshold of the spindles.

Where supra-spinal regulation of the reflex response was powerful enough to augment the response (that is, when a short train of light flashes or clicks was used) a reduction in latency was observed compared with control responses (Tables III and VI). Reduced latency with concurrent indications of fusimotor biasing and the observation of unchanged muscle tonus, is consistent with evidence from infra-human experiments (Eldred and Fujimori, 1958; Granit, et al., 1955; Hunt, 1952). Biasing of the intrafusal fibres by fusimotor impulses makes the spindle a much faster and more sensitive receptor but there is no detectable change in the tension of the extrafusal fibres.

The general observation, when strong biasing of the spindle was assumed, was an increased mean amplitude of response, a decrease in latency and an increase in variance compared with control. Sharp, high intensity stimuli were required to achieve this effect, that is, light flashes and clicks; changes in sound level using a tone were not sufficient.

Adaptation and attenuation

The results from the present experiments reveal that there is no increase in alpha motoneurone activity above control level when a long, repetitive train of bilaterally presented visual or auditory stimuli is used, or when a short train of visual stimuli is presented monocularly, especially if the ipsilateral eye is used.

The findings regarding the use of long trains of repetitive stimuli agree with the results in the literature dealing with adaptation. Sokolov (1963) has reported that a repetitive train of the same stimuli results in adaptation of the orientation reflex while Hagbarth and Kugelberg (1958) have been successful in demonstrating the effect in abdominal skin reflexes of normal human Ss, a phenomenon which they ascribed to dampening of internuncial transmission. This partial blockade of descending pathways, probably, is dependent upon the attenuation of activity in the neurones of the RF as Bell and his associates have shown in cats (Bell, et al., 1964). A low level of reticular activity (similar to control)

during treatments C and J would account for spindle sensitivity being no different from treatment A.

The reduction of the augmentation effect from 3 light flashes when monocular presentation was used instead of binocular presentation also agrees fairly well with a previous related finding. Bickford and co-workers have noted an attenuation of the EMG response to click stimuli, in the range from 20 to 40 per cent (Bickford, et al., 1964). In the present experiments, the data (Table IV) show a reduction below the binocular response of 38 to 68 per cent for ipsilateral monocular presentation and of 19 to 45 per cent for contralateral monocular stimulation. No attempt was made to position the light source so that excitation reached a particular hemisphere of the brain, hence the reduced effect during monocular presentation must be the result of a quantitative difference in the number of visual receptors being activated.

Whenever there was reason to believe that activity in the RF was attenuated or reduced, the means, variances and latencies of the reflex responses were not significantly greater than control and on a few occasions were significantly less.

Product-moment correlation coefficients

The difference between the correlation coefficients between the electrical and mechanical responses during control and experimental treatments (irrespective of the type of treatment) was not

significant. There are three sources of evidence to show that the observations for the two sets of 10 trials within a session lie along regression lines which are nearly identical. First, the t-tests for the difference between the slopes of the regression lines are not significant (Table V). Second, the correlation plots for the two variables under control and experimental treatments show a linear relationship with very little scatter (Figures 15 and 17). Third, the correlation coefficient for 20 trials within sessions is not different from that obtained for the two groups of 10 trials taken separately (Tables III and V).

This evidence indicates that fluctuations in fusimotor biasing of spindles over an apparently large range of the arousal continuum, have no effect on the high, positive relationship between the mechanical (maximum force of the isometric contraction) and electrical (impulse of the MAP) responses.

Apparently the degree of fusimotor biasing determines the number of spindles which will be activated (by setting the threshold of the spindles) and, as a consequence, a certain number of motor units on the extrafusal fibres are induced to discharge. Under isometric conditions, the number of motor units which discharge is proportional to the number of extrafusal fibres which contract and the MAP. Hence, the impulse of the isometric contraction and the impulse of the MAP are highly correlated provided the

compliance of the transducer used to record the force of the contraction is low (so that the muscle does not change length) and also provided muscle tonus remains consistent.

CONCLUSION

These experiments have shown that certain kinds of stimuli impinging upon two types of sensory receptors (auditory and visual) produce effects on the phasic stretch reflex. The results obtained, therefore, are not specific to a particular sense modality.

Initial presentations of one type of novel, intermittent stimulus apparently alert the S so that there is a general sensitisation of other types of receptors, for example, muscle spindles. Stimuli which are 'sharp-edged', harsh in quality and which are presented bilaterally in brief trains are most effective in evoking a high state of arousal. Stimuli which are presented monocularly or as a single change in sound level are not effective in altering the response level.

The finding that bilateral presentation of 3 clicks or 3 light flashes augments the response while more than 30 presentations of these stimuli results in responses which are not different from control, shows that accurate control can be achieved over the reflex response.

The three indices of increased response amplitude and variance with concomitant shortening of latency, when they occur together, seem to provide reliable, indirect indications of fusimotor activity. However, the variance ratio between control and experimental treatments, within sessions, appears to be slightly more sensitive if only one index is required (Tables III and IV).

Provided the S is trained in relaxation and the control level reflex is elicited with a stretch stimulus which is just above threshold, the alpha motoneurons seem to monitor accurately the activity of the fusimotor neurones. The arousal and attenuation of the reticular neurone activity brought about by the types of intermittent bilateral stimulation used result in similar response characteristics in the fusimotor neurones. The consequent alteration of spindle sensitivity is reflected in the alpha motor response in a phasic stretch reflex.

It seems reasonable to believe that with the kinds of precautions taken in the present experiments, the phasic reflex response may be used as an indicator of fusimotor activity which, in turn, reflects the activity in the facilitating and inhibiting systems of the supra-spinal regions of the CNS.

CHAPTER VIII

THE EFFECT OF MENTAL ACTIVITY
ON THE PATELLAR REFLEX

The effect of various types of stimuli impinging upon visual and auditory receptors, or exteroceptors, was reported in Chapter VII. Experiments will be described in Chapter IX which deal with proprioceptive stimuli and their effect on the reflex. The focus of attention in this chapter is on the possible effects of mental activity on the reflex. This kind of investigation has been done before but the reasons for repeating it are that there is contradictory evidence about the effect and also, a further test of the three indices of fusimotor activity can be made during this treatment.

Studies with human subjects

Lombard (1887) found that mental arithmetic (a difficult multiplication of two numbers) did not augment the reflex in a significant way unless the S was asked to work very quickly so that emotions were aroused.

However, Tuttle (1924 b) reported a contrary finding. Comparisons were made between 'passive' periods when the S sat quietly with eyes closed, and 'active' periods during which mental arithmetic and calculations made with the aid of paper and pencil were carried out. The average increase in the size

of the patellar reflex for the seven Ss was about 10 times during mental activity and, also, the responses became more variable compared with the passive period. Tuttle's report showed that the augmentation during calculations made with the eyes open to use pencil and paper, was about 3 times the size of that observed during mental arithmetic when the eyes were closed.

Presumably, this difference in size of the response is the result of allowing contraction of remote muscles and visual stimulation during writing the figures to increase the arousal of the RF, with consequent activation of the fusimotor and alpha systems. Tuttle (1924 b) concluded that mental activity 'increases muscle tonus as exhibited by the knee-jerk' although there is no evidence that objective estimates of tonus were made.

On this point, Golla and Antonovitch (1929), measured tonus and the knee-jerk simultaneously during tasks such as the addition of columns of figures, reading silently or aloud, and motor performance (such as holding a rod in the centre of a small circle of wire). Their results showed that there was a simultaneous increase in muscle tonus and size of the reflex with mental activity. They also noted 'an astonishing degree of variability in the individual responses' such that on occasions they checked the reliability of the apparatus. Tuttle (1924 a) had proposed fluctuations in cerebation as the reason for the large variance but Golla and Antonovitch (1929), in an adumbration of later

theories, postulated a sub-cortical mechanism to account for the fact that some variability was observed at the earliest return of the reflex following ether anaesthesia.

Emery (1931) was able to demonstrate both facilitation and inhibition of the knee-jerk by asking Ss to imagine they were kicking forward or kicking backward. His explanation of this result was that the tonus of the quadriceps muscle is increased when the S imagines he is pushing forward whereas the tonus of the hamstring muscles is increased and the quadriceps is inhibited when the S imagines he is pushing backwards. However, plausible as this explanation may be, Emery was unable to demonstrate augmentation with mental activity in a later report (Emery, 1944). In the experiment Emery asked his Ss (1220 males, 36 females) to use a formula to make additions; 'The sum of 1 to any number x is $(\frac{x}{2} + \frac{1}{2})x$ '. The Ss were instructed to try the formula for the numbers 1 to 10 and compare the answers with addition. Analysis of the results showed that no change occurred with 9 per cent of the men and 3 per cent of the women while 30 per cent and 22 per cent of men and women, respectively, decreased the reflex response during mental calculations. Where augmentation was observed it was significant only for the men.

More recent investigations into the effect of mental calculations (in the form of multiplication of two digit numbers) have been made by Paillard (1959).

The results showed that the mechanically elicited Achilles reflex was increased in amplitude and variability of response whilst the H-reflex, although augmented, remained fairly constant. This finding seems to indicate that the main effect of augmentation, under this treatment, is by way of the fusimotor system. Although no statistics were presented in this report, there seems to be no doubt that the mechanically elicited reflex was augmented significantly during the period of mental calculations.

Relevant Neurophysiology

Centrifugal projections to the RF are known to exist (Magoun, 1958; Lindsley, 1961). However, the work of Granit and Kaada (1953) has shown that whilst muscle spindle discharges can be regulated accurately from the RF, less rigid control could be achieved from the motor cortex. In addition, the stimulus-intensities required to produce these effects were different. Stimulation of the facilitatory regions of the RF could cause acceleration of gamma activity with ease and at intensities below those necessary to elicit responses in alpha motoneurons. However, an increase in gamma discharge on stimulation of the motor cortex occurred irregularly and, if the intensity of the stimulus was increased in an attempt to obtain consistent effects, the alpha motoneurons discharged (Granit and Kaada, 1953).

This evidence indicates that centrifugal control of the muscle spindles takes place mostly by way of the RF.

Rationale for the present experiment

Reports on the effect of mental activity on the reflex obviously give conflicting results. The reasons for the lack of consistency are partly in differences in methods of recording (for example, isotonic or isometric) and partly in the lack of adequate controls (for example, muscle tonus often was reported to be greater under experimental conditions than under control conditions).

The present experiment was designed to overcome some of the deficiencies in control. Data were rejected if a significant difference in muscle tonus was found between control and experimental conditions. The S was required to sit still with the eyes masked and mentally to make arithmetical calculations; no written work was permitted. Hence, the results were not contaminated with the effects of changing visual stimulation and irrelevant muscular activity.

Subjects

Four normal adult Ss (2 males, 2 females) participated in the experiment.

Apparatus

As previously described.

Experimental design

The experimental sessions consisted of

- (i) 5 control trials, S relaxed with eyes masked (treatment A)
- (ii) 10 trials as for A but the S was required to use the formula ${}_1\Sigma_x = \left(\frac{x}{2} + \frac{1}{2}\right)x$ to sum from 1 to any number commencing at 20 and was asked to work mentally as rapidly and accurately as possible (treatment L)
- (iii) treatment A repeated.

At the completion of the first application of treatment A the E quietly instructed the S to begin calculations. About 20 seconds were allowed before treatment L began and when the 10 trials were completed the S was told to stop. About 20 seconds were allowed before the second application of treatment A to allow the S to return to a state of relaxation.

In view of the conflicting results in the literature, no predictions were made for the present experiment. The aim was to observe the mean, variance and latency of the responses under control and experimental treatments.

RESULTS

Table VII shows the results for the independent and dependent variables, and the data relevant to

TABLE VII

DATA RELEVANT TO THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND THE DEPENDENT VARIABLES (LATENCY, MAXIMUM FORCE OF ISOMETRIC CONTRACTION AND IMPULSE OF THE MUSCLE ACTION POTENTIAL) DURING CONTROL (A) AND EXPERIMENTAL TREATMENT OF MENTAL CALCULATIONS (L) DURING WHICH THE SUBJECT USED THE FORMULA $\sum_{i=1}^n x = (\frac{n}{2} + \frac{1}{2})x$ TO SUM

SETS OF SUCCESSIVE NUMBERS.

| Subject | Sequence | Treatment | Peak Force on Ligament (kg) | | Latency (msec) | | | Maximum Force of Isometric Contraction (kg) | | | | Impulse of M.A.P. (uV sec) | | | | Correlation Max. Force and M.A.P. | | Z test for difference between correlation coefficients | t test for difference between slopes of regression lines |
|---------|----------|-----------|-----------------------------|---------------|----------------|------|------|---|---------|---------|--------|----------------------------|---------|----------------|----------------|-----------------------------------|----------|--|--|
| | | | \bar{x} | t | \bar{x} | t | df | \bar{x} | t | R^2 | F | \bar{x} | t | R^2 | F | r | N | | |
| A.M. | ALA | Control | 2.14 | 0.63 | 20.1 | 0.23 | 18 | 1.12 | 0.87 | 0.38 | 1.61 | 0.86 | 0.69 | 0.36 | 1.01 | 0.936 | 10 | 1.59 | - |
| | | Exper. | 2.16 | | 20.0 | | | 1.39 | | 0.61 | | 1.04 | | 0.36 | | 0.988 0.961 | 10 20 | | |
| | ALA | Control | 2.13 | 0.39 | 20.4 | 0.57 | 18 | 0.83 | 1.61 | 0.14 | 2.29 | 1.47 | 2.03 | 0.39 | 1.43 | 0.979 | 10 | 0.63 | 2.07 |
| | | Exper. | 2.14 | | 20.2 | | | 1.16 | | 0.31 | | 2.10 | | 0.57 | | 0.987 0.967 | 10 20 | | |
| | ALA | Control | 1.93 | 0.54 | not available | | | 1.76 | 1.16 | 0.36 | 1.34 | 1.58 | 0.37 | 0.23 | 1.46 | 0.939 | 10 | 1.09 | 0.71 |
| Exper. | 1.94 | | | | | 1.43 | | 0.48 | | 1.51 | | 0.16 | | 0.816 0.854 | 10 20 | | | | |
| ALA | Control | 1.79 | 0.62 | not available | | | 0.45 | 1.78 | 0.09 | 3.65* | 0.40 | 1.81 | 0.16 | 2.84 | 0.935 | 10 | 1.69 | 1.49 | |
| Exper. | 1.83 | | | | | 0.82 | | 0.33 | | 0.85 | | 0.45 | | 0.994 0.971 | 10 20 | | | | |
| LAL | Control | 1.80 | 0.28 | not available | | | 1.72 | 2.23* | 0.79 | 13.8*** | 2.99 | 3.06** | 1.39 | 7.14** | 0.944 | 10 | 0.15 | 0.84 | |
| Exper. | 1.79 | | | | | 1.08 | | 0.06 | | 1.79 | | 0.19 | | 0.928 0.900 | 10 20 | | | | |
| B.H. | ALA | Control | 2.25 | | not available | | | 0.27 | 1.14 | 0.03 | 9.30** | 0.39 | 1.18 | 0.31 | 3.34* | 0.939 | 10 | 1.13 | - |
| | | Exper. | 2.26 | 0.29 | | | | 0.48 | | 0.31 | | 0.83 | | 1.03 | 0.984 0.993 | 10 20 | | | |
| | ALA | Control | 1.95 | 1.35 | 19.3 | 1.19 | 6 | 0.42 | 0.66 | 0.04 | 1.89 | 0.65 | 1.50 | 0.07 | 2.44 | 0.892 | 10 | 0.66 | |
| Exper. | 1.92 | | 18.9 | | | 0.37 | | 0.02 | | 0.50 | | 0.03 | | 0.789 0.848 | 10 20 | | | | |
| ALA | Control | 1.28 | 0.76 | 20.8 | 1.22 | 11 | 0.38 | 0.28 | 0.24 | 1.60 | 2.82 | 0.28 | 9.85 | 1.54 | 0.985 | 10 | 0.38 | - | |
| Exper. | 1.29 | | 21.3 | | | 0.33 | | 0.15 | | 2.46 | | 6.39 | | 0.990 0.989 | 10 20 | | | | |
| W.R. | ALA | Control | 2.40 | | not available | | | 0.27 | 4.79*** | 0.01 | 8.79** | 0.29 | 5.42*** | 0.01 | 6.95** | 0.803 | 10 | 1.19 | 1.11 |
| | | Exper. | 2.40 | 0.00 | | | | 0.74 | | 0.09 | | 0.65 | | 0.04 | | 0.937 0.634 | 10 20 | | |
| | ALA | Control | 2.18 | 1.61 | not available | | | 0.30 | 1.86 | 0.03 | 1.16 | 0.65 | 2.41* | 0.09 | 1.60 | 0.944 | 10 | 1.15 | - |
| Exper. | 2.25 | | | | | 0.44 | | 0.02 | | 1.02 | | 0.15 | | 0.816 0.885 | 10 20 | | | | |
| ALA | Control | 2.08 | 1.26 | 23.6 | 1.03 | 7 | 0.34 | 1.43 | 0.04 | 3.21* | 0.71 | 1.63 | 0.11 | 5.07* | 0.969 | 10 | 0.63 | - | |
| Exper. | 2.05 | | 23.4 | | | 0.53 | | 0.12 | | 1.12 | | 0.53 | | 0.984 0.861 | 10 20 | | | | |
| G.B. | ALA | Control | 1.67 | 0.89 | 20.3 | 0.01 | 11 | 0.99 | 2.19* | 0.83 | 1.20 | 1.23 | 1.28 | 0.19 | 1.03 | 0.868 | 10 | 1.15 | - |
| | | Exper. | 1.68 | | 20.3 | | | 0.72 | | 0.69 | | 0.99 | | 0.18 | | 0.941 0.896 | 10 20 | | |

Probability levels: *P < 0.05, **P < 0.01, ***P < 0.001

the product-moment correlations between the mechanical and electrical responses.

There were no significant differences between the means of the peak force on the ligament for control and experimental treatments within sessions.

The effect of mental calculations on the dependent variables

On no occasion was there a significant difference between treatments for latency readings. On only one occasion each did the maximum force of the isometric contraction and the impulse of the MAP, show significance for differences between means. The number of significant increases in variance over control treatment responses was slightly higher (Sign test, $p < 0.14$).

On two occasions there were significant reductions in mean responses during treatment L compared with control for the mechanical response. These were associated with reduced variance (significant on one occasion).

The effect of mental calculations on correlation coefficients

High, product-moment correlation coefficients were found between the maximum force of the isometric contraction and the impulse of the MAP in control and experimental treatments. Without exception there was no significant difference between correlation coefficients for the two treatments within sessions.

Random checks showed that there was no significant difference between the slopes of the regression lines within sessions.

DISCUSSION

The results of this experiment show that, under the controls used, mentally calculated problems in arithmetic have no consistent effect on the patellar reflex. Across all sessions and Ss three out of twelve differences for the impulse of the MAP were significant. Not more than one comparison was significant for any S and the significant differences which were obtained varied in sign.

This finding confirms the work of Emery (1944). His experiments were conducted in a quiet room and the formula used for the mental calculations was given beforehand so that auditory stimuli (in the form of a series of posed questions) were excluded. Under these conditions, Emery's results showed a wide range from negative to positive augmentation very much like the results in the present experiment. Lombard (1887) who controlled similar variables, also found that mental arithmetic did not seem to affect the reflex unless an endeavour was made to work at speed.

When a significant increase in the reflex during mental activity has been reported, the main reason seems to have been an increase in muscle tonus during

the experimental treatment; Tuttle (1924 b), Golla and Antonovitch (1929) and Emery (1931) all have noted an increase in tonus during mental work so that the physical state of the muscle was different to that during control treatment in their experiments. Tuttle (1924 b) and Golla and Antonovitch (1929) gave arithmetical tasks which also involved the S in visual stimulation and remote muscular activity (writing down the answers to problems) during the experimental period. Under these circumstances, it is not legitimate to attribute the effects obtained to cognitive activity alone because muscular activity in the arms, changes in muscle tonus and certain kinds of visual stimulation have effects on the reflex as this thesis shows.

There are insufficient details in Paillard's report to assess the methods used to control environmental and organismic stimuli (Paillard, 1959). However, the problems in arithmetic were posed to the S verbally so that auditory stimuli interacted with the experimental treatment and, therefore, the results are confounded with an extraneous variable.

The infra-human experiments by Granit and Kaada (1953) have shown that unreliable control was achieved over discharge in ventral root filaments displaying alpha and gamma spikes by stimulation of the motor cortex and French (1960), in reviewing the relevant literature has concluded that reticulospinal pathways exhibit some degree of independence from cortical influences. On these grounds, the results obtained

by Lombard (1887) and Emery (1944) using some control over relevant variables, most probably contain accurate information about the effects of cortical activity on the human phasic stretch reflex.

The general findings of the present experiment show that when relevant variables such as:

- (a) muscle tonus
- (b) exteroceptive stimuli (for example, auditory and visual stimulation)
- (c) proprioceptive stimuli (contraction of remote muscles)

are held as constant as possible between control and experimental treatments, mental calculations, performed rapidly, have no consistent effect on the patellar reflex.

CHAPTER IX

THE EFFECT OF CERTAIN PROPRIOCEPTIVE STIMULI
ON THE PATELLAR REFLEX DURING EXPERIMENTAL CONTROL
OVER SUPRA-SPINAL INFLUENCES

Evidence has been presented for the effects of exteroceptive stimulation and mental activity on the reflex. Accurate control of the response was possible with certain kinds of the former stimuli but inconsistent effects were found with the latter.

This chapter deals with proprioceptive stimuli which are evoked by the action of the body itself. The three indices of fusimotor activity will be observed under experimental conditions designed to exert control over supra-spinal influences mainly by natural, behavioural methods. However, a drug, Myanesin, presented favourable circumstances for additional control of pathways descending from the CNS. For this reason it was used in this experiment as a further means of assessing the validity of the indices of fusimotor activity.

Rationale for the experiment

Until recently the evidence gained by comparisons between electrical (H reflex) and mechanical (tendon jerk) stimulation during the JM has indicated that the fusimotor system plays the paramount role in facilitating monosynaptic reflexes by heightening the sensitivity of the muscle spindles. More recent

evidence, making use of the same techniques, has raised the question that it may not be necessary to postulate facilitation during the JM to be solely the result of fusimotor biasing of the spindle. This report deals with experiments which examine this question by studying the effects of the JM during several conditions (other than electrical stimulation) designed to control supra-spinal influences differentially.

Landau and Clare (1964) have pointed out that the use of the Hoffmann technique of electrical stimulation of muscle afferents, by which the effect of the spindle receptor may be isolated from the motor response, has enabled investigators to infer that the facilitation of monosynaptic reflexes during the JM occurred by way of fusimotor alteration of the sensitivity of the spindle. The H reflex seemed resistant to augmentation during the JM (Buller and Dornhorst, 1957; Paillard, 1959) and it was reasonable to assume that the fusimotor neurones, which exclusively innervate the intrafusal fibres of the spindle were responsible for the augmentation phenomenon.

Since 1961 there have been reports of the augmentation of the H reflex by contraction of remote muscles (Benson and Gedye, 1961; Landau and Clare, 1964). In addition, Clare and Landau (1964) have used the technique of differential nerve blockade (Matthews and Rushworth, 1957) to study the effect of the JM on reflexes which had been depressed by the selective

blockade of tonic fusimotor discharge. They found that augmentation of the reflex became more effective and 'when the tendon jerk was absent, even with reinforcement, the depressed H reflex could still be reinforced'.

If the sensitisation of the spindle by way of the fusimotor system is not the sole facilitatory mechanism during the JM, what additional influences could be operating?

Sensory pathways make collateral connections with the reticular formation (Magoun, 1958) so that ascending impulses from activity in remote muscles during the JM would be expected initially to activate the reticular formation which has comprehensive polysynaptic connections with fusimotor neurones (Granit and Kaada, 1953; Appelberg and Emonet-Denand, 1965). Therefore, the level of excitation of the reticular formation is likely to be mirrored in the excitation of fusimotor neurones (Granit, 1957) and, consequently, in the threshold of the spindles. However, descending influences not only affect the extrafusal response indirectly by way of the fusimotor neurones but also partly by direct action on the alpha motoneurones (Rossi and Zanchetti, 1957). Presumably in normal Ss, both these modes of influences operate together on the reflex response (Granit, et al., 1959) when the reticular system is aroused by afferent impulses emanating from active contraction of remote muscles during a JM.

Since some degree of fusimotor tone probably is necessary for the existence of a stretch reflex (Eldred, 1960) and as the discharge in fusimotor neurones constantly fluctuates (Granit and Henatsch, 1956), the biasing of the spindle would be expected to contribute to increased variability of the responses. The data graphed by Benson and Gedye (1961, Figure VIII) support this proposition; there was a significant difference between the mean of the reflex responses for both the tendon jerk and the H reflex ($p < 0.001$, 18 df; each statistic was the mean of 8 observations for 4 Ss) between experimental trials when a remote muscle was contracted, and control trials. However, the F ratio was significant only for the tendon jerk, a finding which is consistent with the proposition that heightened fusimotor activity results in increased variance of reflex responses. Unfortunately, no latency observations were reported.

The responses observed by Paillard (1959) provide specific evidence concerning the postulated relationship between the variance of the mechanically elicited reflex and fusimotor biasing of the spindles. In Paillard's experiment reflexes were elicited simultaneously in the right gastrocnemius (H reflex) and in the left gastrocnemius (tendon jerk) during a JM which involved clenching a fist. The H reflex 'excitability remained unchanged' whilst the mechanically elicited responses displayed large variance which Paillard has attributed to an increase in spindle sensitivity by means of the fusimotor system.

In the experiments reported here, the effect of the JM on the patellar reflex was investigated under several conditions in the expectation that each condition would lead to fusimotor discharge having a differential effect on the response. The four experiments consisted of a comparison of the reflex responses in the following pairs of conditions:

- (i) control, with the S relaxing, and a JM maintained for 1 sec before the tap on the ligamentum patellae,
- (ii) control and a JM maintained for 10 sec,
- (iii) active contraction of rectus femoris (pre-strain) and pre-strain with concurrent execution of a JM for 1 sec, and
- (iv) control and JM (1 sec) in a series of sessions designed to investigate the effect of an inter-neuronal blocking agent, Myanesin (Mephenesin, B.P.C.).

The reasons for these procedures were as follows:

- (a) For the reasons given in Chapter III, it was anticipated that the maintenance of a consistent level of relaxation would be conducive to the reduction of supra-spinal influences and, consequently, to reflex responses having small variance. This would enable clear comparisons to be made between control and experimental results.

- (b) Bowditch and Warren (1890) have reported that the augmentation of the patellar reflex was lost if a JM was continued for more than 2 sec, although Buller and Dornhorst (1957) found that reinforcement persisted up to 6 sec. Since the neurones in the mesencephalic reticular formation are known to respond well to initial sensory stimulation but to attenuate to repetitive stimuli (Bell, et al., 1964), it may be assumed that a JM would result in ascending impulses which would initially augment the reticular response but if the JM were continued, adaptation of reticular neurones would occur. These features of reticular response would be paralleled, as a result of direct and indirect descending influences, by similar characteristics of alpha motoneurone responses. That is, both the mean and variance of the extrafusal responses should be increased and latency decreased during JM (1 sec) conditions but these aspects of the responses during JM (10 sec) conditions should not be different from control responses.
- (c) During active, isometric contraction of the rectus femoris muscle, the spindles would be unloaded because it is thought that the tendons are elastic enough to permit some shortening of the extrafusal

fibres (Eldred, et al., 1953; Granit, 1955a; Hunt and Perl, 1960). Therefore, the tap on the ligament was timed to occur just as the S brought the extensor force up to the required amount of pre-strain; the assumption being that the response would be elicited before the fusimotor system (which would become active when voluntary contraction began) could adjust the slack in the intrafusal fibres to the new length of the extrafusal fibres. Under these circumstances, the effect of fusimotor biasing would be minimised and a decrease in the variance of responses compared with control responses would be expected. Also, if the increased sensitisation of the spindle by fusimotor activity were the main source of influence, no significant augmentation should occur between pre-strain trials and pre-strain with JM trials.

(d) The use of Myanesin (Mephenesin, B.P.C.)

(i) Site of action

Mephenesin acts primarily on the spinal cord and there is general agreement that it has a depressant effect on spinal neurones including inter-neurones (Berger, 1947, 1949; Henneman, et al., 1949; Funderburk, et al., 1953; Voorhoeve, 1960). Mephenesin

acts rapidly to reduce polysynaptic transmission but monosynaptic pathways are not affected (Berger, 1947, 1949; Voorhoeve, 1960).

Hence, reticulo-spinal pathways which carry nearly all extra-pyramidal influences from supra-spinal levels of the CNS to the cord, are depressed (Henneman, et al., 1949; Kaada, 1950; Funderburk, et al., 1953; Domino, 1956).

Granit and Holmgren (1955) and Hunt and Paintal (1958) have observed depression of background activity in fusimotor neurones after administration of small doses of Myanesin.

(ii) Effect on the stretch reflex

The effects of reticular stimulation on the patellar reflex are depressed by Myanesin (Domino, 1956) and, in fact, both facilitatory and inhibitory influences arriving at spinal cells from all levels of the CNS are decreased (Henneman, et al., 1949).

Under these circumstances, it is not surprising to find that irregular knee-jerk responses are eliminated by Myanesin and the reflex becomes quite uniform (Berger, 1947).

Myanesin also has the advantage of being rapidly and thoroughly absorbed from the intestinal tract following oral administration (Berger, 1947).

In the present experiments, the use of Myanesin was expected to attenuate both the direct and indirect influences descending from supra-spinal levels of the CNS. Under these circumstances, the JM (1 sec) was expected to have no effect on the mean, variance and latency of the responses during the peak drug effect compared with control responses.

Subjects

Four normal adult Ss (2 males, 2 females) participated in the main sessions. One male and one female were studied in the pre-strain experiments and two females in the drug experiment. All had participated in previous experiments and were well trained in relaxation.

Apparatus and method

The apparatus used was the same as that previously described.

In addition, a meter which registered the force at the ankle-cuff, was placed in front of the S at eye-level. After some practice, the S could report to E as the leg was being extended so that the

pendulum-hammer could be released to tap the ligament as the required force was reached. Trials which failed to meet this criterion were discarded.

The JM used was a force of 15 kg exerted by both hands with dynamometers.

The drug (Myanesin) and the placebo (calcium carbonate) were administered in powdered form. Dosage was 1gr taken orally.

Eye masks were not used in this experiment because the S was required to observe readings on the dials mentioned above. However, the room illumination was reduced to about 27 lumens/sq metre. A stiff cardboard screen was placed across the arm rests of the chair to obscure the S's view of the pendulum-hammer.

Experimental design

The main experiment to examine the effect of a JM maintained for 1 sec and for 10 sec consisted of:

- (i) 5 control trials with the S relaxed, eyes open looking at the dials of the hand dynamometers held loosely in his hands (treatment A); 10 experimental trials with the application of a JM for 1 sec before the tap on the ligament (treatment F); and finally, treatment A repeated.

- (ii) 5 trials under treatment F; 10 control trials under treatment A; and finally 5 trials under treatment F to test for possible sequential effects of the treatments, and
- (iii) 5 trials under treatment A; 10 trials with the application of a JM for 10 sec before the tap on the ligament (treatment G); and finally, treatment A repeated.

The drug experiment consisted of AFA treatments as described in (i) above under the following six conditions: pre-drug, post-drug ($\frac{1}{2}$ h), post-drug ($1\frac{1}{2}$ h), pre-placebo, post-placebo ($\frac{1}{2}$ h), and post-placebo ($1\frac{1}{2}$ h).

The pre-strain experiment consisted of a counter-balanced design of ordinary pre-strain trials and pre-strain with JM (1 sec) trials. With one S (BH) several zero pre-strain (that is, treatment A) trials were added to compare the variance with that during $1\frac{1}{2}$ kg pre-strain trials.

The impulse of the MAP was observed as the principal dependent variable in the experiments. The mean, variance and latency of the responses were examined under control and experimental treatments. Also, the product-moment correlation coefficients for treatments A, F and G were calculated to find out whether marked changes occurred as a result of the different experimental treatments.

RESULTS

Independent variable

The range of the peak force of the tap on the ligament was 1.01 kg to 2.66 kg.

No significant difference existed between the means of control and experimental trials (Tables VIII and IX).

Augmentation and adaptation

Without exception for the four Ss there was a significant increase in mean impulse of the MAP for JM (1 sec) conditions, whilst there was no significant increase during JM (10 sec) conditions. Table VIII gives data for all Ss and Figure 18 shows examples of the simultaneous EMG and force records for the control and two JM conditions for subject B.H. High, positive correlations were observed between electrical and mechanical responses under all treatments (Figures 19 and 20, and Table VIII).

A significant increase in the variance of the impulse of the MAP during JM (1 sec) conditions compared with control conditions, but no increase during JM (10 sec) conditions, was observed without exception. Similar results were obtained for the maximum force of the isometric contraction except that the variance, while being in the predicted direction, was not always significantly greater in treatment F compared with treatment A (Table VIII).

TABLE IIX
 DATA RELEVANT TO THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND THE DEPENDENT VARIABLES
 (LATENCY, MAXIMUM FORCE OF THE ISOMETRIC REFLEX CONTRACTION, AND THE IMPULSE OF THE MUSCLE ACTION POTENTIAL) DURING
 CONTROL (A) AND EXPERIMENTAL TREATMENTS OF A JENDRASSIK MANOEUVRE MAINTAINED FOR 1 SEC (F) AND A J.M. MAINTAINED
 FOR 10 SEC (G) BEFORE THE TAP ON THE LIGAMENT.

| Subject | Sequence | Treat- ment | Peak Force on Ligament (kg) | | Latency (msec) | | | Maximum Force of Isometric Contraction (kg) | | | | Impulse of M.A.P. (μ V sec) | | | | Corre- lation Max. Force & M.A.P. | N |
|---------|----------|----------------|-----------------------------------|------|-------------------|---------|----|---|---------|----------------|---------|-------------------------------------|---------|----------------|--------|---|----|
| | | | \bar{x} | t | \bar{x} | t | df | \bar{x} | t | S ² | F | \bar{x} | t | S ² | F | | |
| W.R. | AFA | Control | 2.56 | 1.48 | Not available | | | 0.24 | 6.05*** | 0.04 | 2.97 | 0.48 | 4.66*** | 0.11 | 9.07** | 0.961 | 10 |
| | | Exper. | 2.52 | | | | | 0.99 | | 0.11 | | 2.05 | | 1.03 | | 0.990 | 10 |
| | AGA | Control | 1.97 | 0.79 | 22.8 | 1.19 | 14 | 0.19 | 1.19 | 0.01 | 2.09 | 1.17 | 2.08 | 0.36 | 2.62 | 0.678 | 10 |
| | | Exper. | 1.95 | | 22.5 | | | 0.26 | | 0.02 | | 1.93 | | 0.95 | | 0.615 | 10 |
| | FAF | Control | 1.66 | 1.77 | 21.8 | 3.03* | 12 | 0.14 | 6.56*** | 0.01 | 21.8*** | 0.48 | 5.09*** | 0.08 | 10.2** | 0.971 | 10 |
| | | Exper. | 1.74 | | 21.1 | | | 1.02 | | 0.17 | | 2.32 | | 0.83 | | 0.908 | 10 |
| M.D. | AFA | Control | 1.35 | 0.86 | 23.4 | 3.17** | 17 | 0.79 | 3.51** | 0.17 | 3.52* | 0.78 | 3.71** | 0.15 | 7.72** | 0.904 | 10 |
| | | Exper. | 1.33 | | 20.8 | | | 1.77 | | 0.61 | | 2.12 | | 1.16 | | 0.954 | 10 |
| | AGA | Control | 1.17 | 0.76 | 23.3 | 0.53 | 18 | 0.64 | 0.95 | 0.36 | 1.54 | 1.01 | 0.76 | 0.61 | 2.06 | 0.980 | 10 |
| | | Exper. | 1.21 | | 22.8 | | | 0.87 | | 0.23 | | 1.24 | | 0.29 | | 0.810 | 10 |
| | FAF | Control | 1.66 | 1.14 | 23.8 | 0.84 | 11 | 0.66 | 2.98 | 0.36 | 2.04 | 0.31 | 3.09** | 0.05 | 6.29** | 0.969 | 10 |
| | | Exper. | 1.68 | | 22.8 | | | 1.64 | | 0.73 | | 0.89 | | 0.30 | | 0.888 | 10 |
| B.H. | AFA | Control | 1.95 | 1.48 | 19.3 | 2.99* | 9 | 0.42 | 5.69*** | 0.04 | 2.56 | 0.65 | 5.14*** | 0.07 | 8.00** | 0.892 | 10 |
| | | Exper. | 1.92 | | 18.1 | | | 1.07 | | 0.10 | | 1.90 | | 0.53 | | 0.968 | 10 |
| | AGA | Control | 1.42 | 0.03 | 20.5 | 0.89 | 18 | 0.38 | 0.23 | 0.05 | 1.70 | 1.35 | 0.29 | 0.65 | 1.17 | 0.982 | 10 |
| | | Exper. | 1.42 | | 20.7 | | | 0.41 | | 0.08 | | 1.25 | | 0.56 | | 0.957 | 10 |
| | FAF | Control | 1.58 | 1.17 | 21.6 | 3.35** | 15 | 0.30 | 6.72*** | 0.05 | 5.78** | 1.13 | 7.46*** | 0.88 | 4.47* | 0.992 | 10 |
| | | Exper. | 1.55 | | 20.3 | | | 1.49 | | 0.27 | | 6.28 | | 3.91 | | 0.989 | 10 |
| R.R. | AFA | Control | 1.43 | 0.80 | 20.1 | 2.92** | 18 | 1.18 | 5.99*** | 0.09 | 2.88 | 2.84 | 6.26*** | 0.47 | 8.38** | 0.955 | 10 |
| | | Exper. | 1.45 | | 19.2 | | | 2.26 | | 0.25 | | 6.78 | | 3.49 | | 0.964 | 10 |
| | AGA | Control | 1.83 | 1.12 | 20.4 | 0.03 | 17 | 2.09 | 0.91 | 0.78 | 3.63* | 5.72 | 1.65 | 3.39 | 2.99 | 0.942 | 10 |
| | | Exper. | 1.80 | | 20.4 | | | 2.37 | | 0.21 | | 6.83 | | 1.14 | | 0.941 | 10 |
| | FAF | Control | 1.35 | 0.46 | 20.1 | 4.86*** | 15 | 0.59 | 6.53*** | 0.06 | 4.62* | 0.96 | 7.29*** | 0.24 | 6.93** | 0.938 | 10 |
| | | Exper. | 1.36 | | 18.7 | | | 1.74 | | 0.25 | | 4.11 | | 1.64 | | 0.923 | 10 |

Probability levels: *P < 0.05, **P < 0.01, ***P < 0.001

TABLE IX
 DATA FOR THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND THE DEPENDENT VARIABLES
 (IMPULSE OF THE MUSCLE ACTION POTENTIAL AND LATENCY) DURING CONTROL AND JENDRASSIK MANOEUVRE (1 SEC)
 CONDITIONS FOR DRUG (MYANESIN) AND PLACEBO TREATMENTS.

| Treatment | Condition | SUBJECT B.H. | | | | | | | | | | SUBJECT M.D. | | | | | | | | | |
|---------------------|-------------|--------------|-----------------------------|------|---|---------|----------------|-------|----------------|---------|----|--------------|-----------------------------|------|---|---------|----------------|--------|----------------|---------|----|
| | | N | Peak Force on Ligament (kg) | | Impulse of Muscle Action Potential (μ V sec) | | | | Latency (msec) | | | N | Peak Force on Ligament (kg) | | Impulse of Muscle Action Potential (μ V sec) | | | | Latency (msec) | | |
| | | | \bar{x} | t | \bar{x} | t | S ² | F | \bar{x} | t | df | | \bar{x} | t | \bar{x} | t | S ² | F | \bar{x} | t | df |
| Pre-drug | Control | 10 | 1.51 | 0.60 | 3.20 | 6.77*** | 2.44 | 1.45 | 20.8 | 2.92* | 15 | 10 | 1.39 | 1.46 | 1.08 | 7.07*** | 0.50 | 7.90** | 21.5 | 7.18*** | 15 |
| | J.M.(1 sec) | 10 | 1.49 | | 8.47 | | 3.54 | | 20.1 | | | 10 | 1.45 | | 5.81 | | 3.97 | | 19.4 | | |
| Post-drug (½ h) | Control | 10 | 1.63 | 1.64 | 4.47 | 1.16 | 6.89 | 1.22 | 20.7 | 1.95 | 16 | 10 | 1.47 | 0.13 | 5.29 | 0.79 | 10.5 | 1.63 | 20.3 | 0.74 | 13 |
| | J.M.(1 sec) | 10 | 1.61 | | 5.77 | | 5.65 | | 19.8 | | | 8 | 1.48 | | 4.19 | | 6.49 | | 20.2 | | |
| Post-drug (1½ h) | Control | 10 | 1.49 | 0.61 | 1.98 | 5.96*** | 1.17 | 3.49* | 21.6 | 5.81*** | 17 | 10 | 1.29 | 1.69 | 1.31 | 4.39*** | 0.31 | 8.93** | 22.8 | 4.23** | 13 |
| | J.M.(1 sec) | 10 | 1.48 | | 6.32 | | 4.10 | | 19.6 | | | 10 | 1.39 | | 3.75 | | 2.76 | | 20.2 | | |
| Pre-placebo | Control | 10 | 1.53 | 0.92 | 3.97 | 2.89** | 2.73 | 2.81 | 19.3 | 2.48* | 15 | 10 | 1.42 | 1.95 | 1.62 | 9.42*** | 0.84 | 4.54* | 21.2 | 3.09** | 18 |
| | J.M.(1 sec) | 10 | 1.52 | | 6.91 | | 7.66 | | 18.3 | | | 10 | 1.49 | | 8.04 | | 3.81 | | 19.3 | | |
| Post-placebo (½ h) | Control | 10 | 1.47 | 0.50 | 1.88 | 2.94** | 1.68 | 2.66 | 20.6 | 2.46 | 14 | 10 | 1.46 | 1.48 | 1.35 | 6.90*** | 0.77 | 5.96** | 21.4 | 2.94* | 15 |
| | J.M.(1 sec) | 10 | 1.49 | | 4.19 | | 4.47 | | 19.5 | | | 10 | 1.43 | | 6.54 | | 4.58 | | 19.3 | | |
| Post-placebo (1½ h) | Control | 10 | 1.69 | 0.87 | 5.32 | 2.67* | 0.97 | 1.99 | 20.4 | 0.75 | 18 | 10 | 1.34 | 0.36 | 1.54 | 8.79*** | 1.44 | 2.23 | 21.3 | 3.77** | 16 |
| | J.M.(1 sec) | 10 | 1.66 | | 6.76 | | 1.92 | | 20.3 | | | 10 | 1.35 | | 7.53 | | 3.22 | | 19.7 | | |

Probability levels: *P < 0.05, **P < 0.01, ***P < 0.001

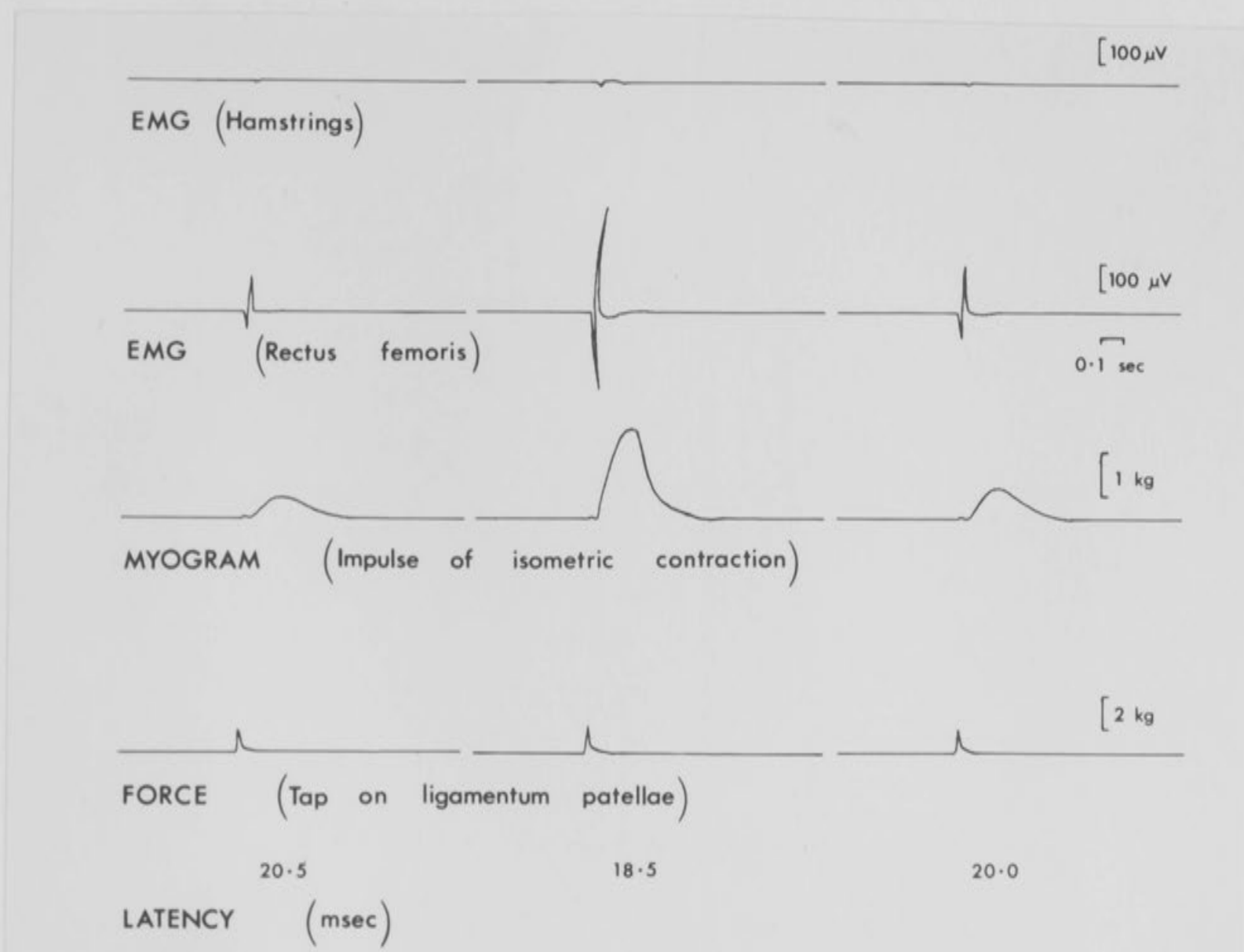


Figure 18

Electromyograms, force and latency records of the patellar reflex response during a control trial (left), during a JM (1 sec) trial (centre) and during a JM (10 sec) trial (right). Subject B.H.

Force of the isometric contraction and the amplitude of the EMG from rectus femoris in the three trials were: Control, $\bar{x} = 0.892$; JM (1 sec), $\bar{x} = 0.876$; JM (10 sec), $\bar{x} = 0.876$. Subject B.H.

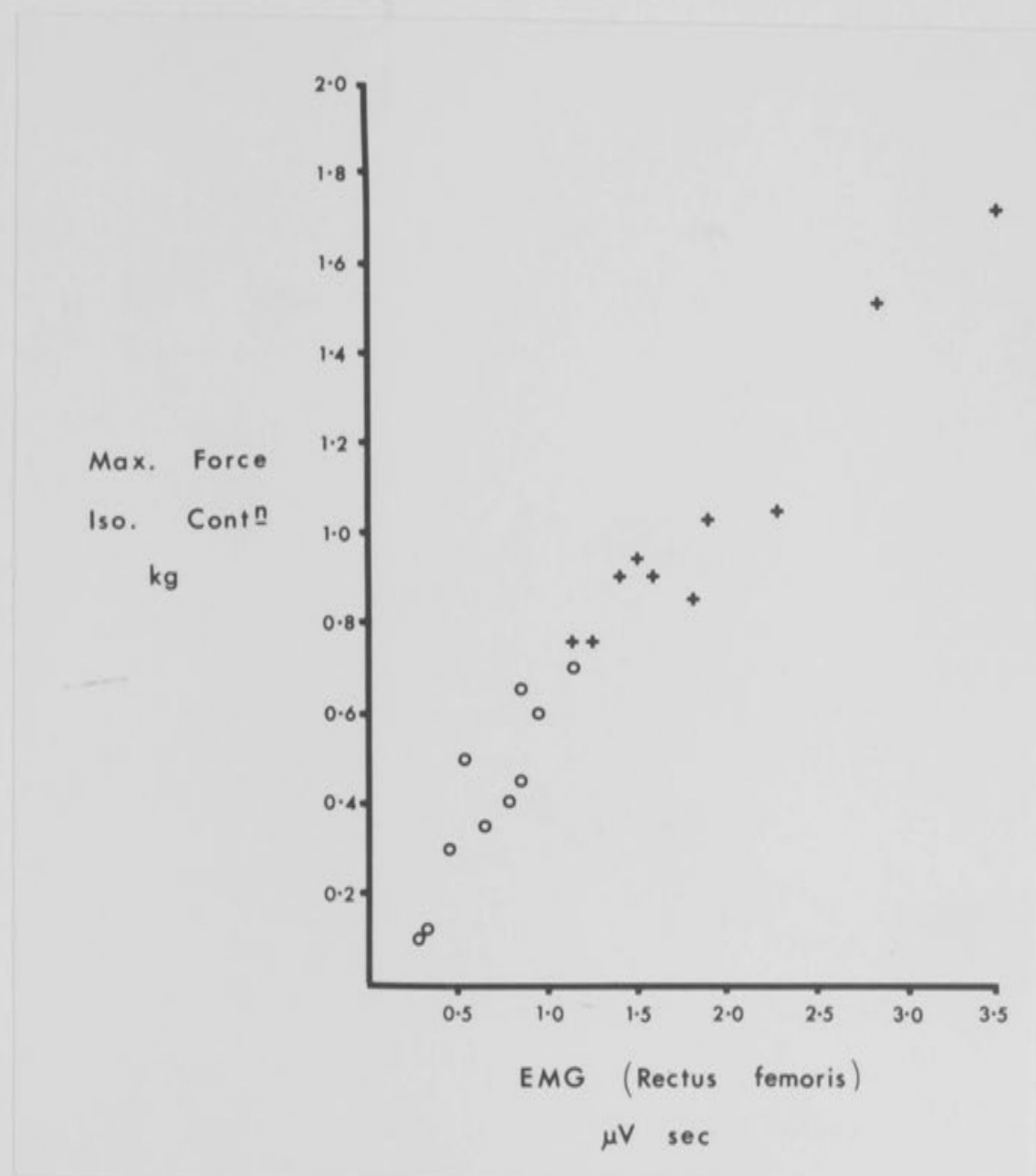


Figure 19

Graph to show the relationship between the maximum force of the isometric contraction and the impulse of the MAP from rectus femoris in the patellar reflex
 o Control, $r = 0.892$; + JM (1 sec), $r = 0.968$.
 Subject B.H.

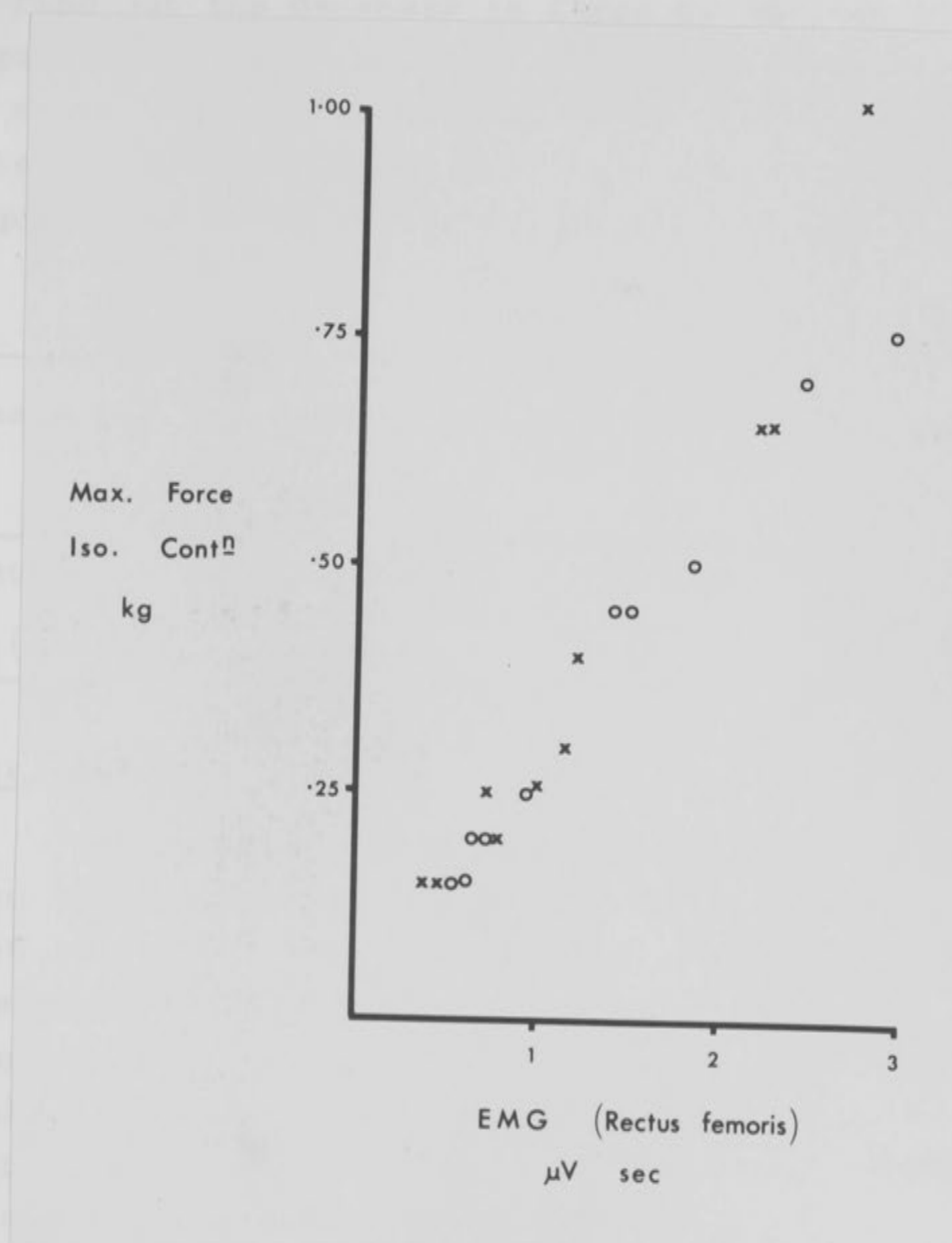


Figure 20

Graph to show the relationship between the maximum force of the isometric contraction and the impulse of the MAP from rectus femoris in the patellar reflex. o Control, $r = 0.982$; x JM (10 sec), $r = 0.957$. Subject B.H.

An extra session was conducted with one S (B.H.) to find out the decrease in force of the tap on the ligament during JM (1 sec) trials which was necessary to match control responses. Table VIIIa gives the relevant data and shows that the change in force required to match the criterion was 760 g.

TABLE VIIIa

| Treatment | Peak force on ligament | Maximum force of isometric contraction | N | <u>t</u> | P |
|------------|---------------------------|--|----|----------|-------------|
| | \bar{x} | \bar{x} | | | |
| Control | 1.75 kg | 0.65 kg | 10 | 0.04 | Not Sig. |
| JM (1 sec) | 0.99 kg | 0.64 kg | 10 | | |

Inter-neuronal blockade

Table IX gives data relevant to the drug and placebo sessions for the two Ss. The pre-drug, post-drug ($1\frac{1}{2}$ h) and all placebo sessions yielded significance-test results similar to those for comparisons of JM (1 sec) and control conditions in Table VIII. There was no placebo effect. Post-drug ($\frac{1}{2}$ h) sessions showed that the JM (1 sec) failed to augment the reflex nor did it increase the variance compared with control. There were no adverse symptoms from the Myanesin and tests for nystagmus were negative.

Pre-strain

The results (Table X) show that

- (i) a significant increase in mean impulse of the MAP was observed between pre-strain and pre-strain with JM (1 sec) treatment (Figure 21),
- (ii) no differences existed between the variances of the two pre-strain conditions, and
- (iii) there was a significant decrease in variance between control and both of the pre-strain conditions when these statistics were available (Subject B.H.).

Reflex latency

Latency observations were not possible, with the apparatus used, during pre-strain conditions. Tables VIII and IX show latencies for the other types of treatment. The general finding was that mean latency, compared with control observations, was reduced significantly by the JM (1 sec) treatment but no differences in mean latency were observed during JM (10 sec) treatment (Figure 22). During the peak effect of the inter-neuronal blocking agent, no difference in mean latency was observed between control and JM (1 sec) trials (Table IX).

TABLE X

DATA FOR THE IMPULSE OF THE MUSCLE ACTION POTENTIAL DURING CONTROL AND TWO EXPERIMENTAL TREATMENTS: (I) PRE-STRAIN AND (II) PRE-STRAIN WITH A JENDRASSIK MANOEUVRE MAINTAINED FOR 1 SEC BEFORE THE TAP ON THE LIGAMENT

| SUBJECT | TREATMENT | N | IMPULSE OF M.A.P. | | | |
|---------|-------------------------------------|----|-------------------|--------------------|----------------|--------------------|
| | | | \bar{x} | t | S ² | F |
| B.H. | Control (zero pre-strain) | 7 | 2.61 | | 1.51 | |
| | 1½ kg pre-strain | 10 | 2.55 | 1.85 ⁺ | 0.38 | 3.97 [*] |
| | 1½ kg pre-strain plus J.M. (1 sec.) | 10 | 3.42 | 3.20 ^{**} | 0.35 | 1.07 |
| B.H. | Control (zero pre-strain) | 9 | 3.94 | | 2.34 | |
| | 1½ kg pre-strain | 7 | 4.29 | 0.58 ⁺ | 0.29 | 8.11 ^{**} |
| | 1½ kg pre-strain plus J.M. (1 sec.) | 7 | 4.92 | 2.66 [*] | 0.11 | 2.67 |
| W.R. | 1 kg pre-strain | 10 | 3.53 | | 0.57 | |
| | 1 kg pre-strain plus J.M. (1 sec.) | 10 | 4.69 | 3.67 ^{**} | 0.54 | 1.05 |
| W.R. | 1 kg pre-strain | 10 | 0.81 | | 0.15 | |
| | 1 kg pre-strain plus J.M. (1 sec.) | 10 | 1.41 | 3.29 ^{**} | 0.08 | 1.92 |

Probability levels: *P < 0.05, **P < 0.01

+ This statistic is not applicable, in this context, because muscle tone changed between treatments.

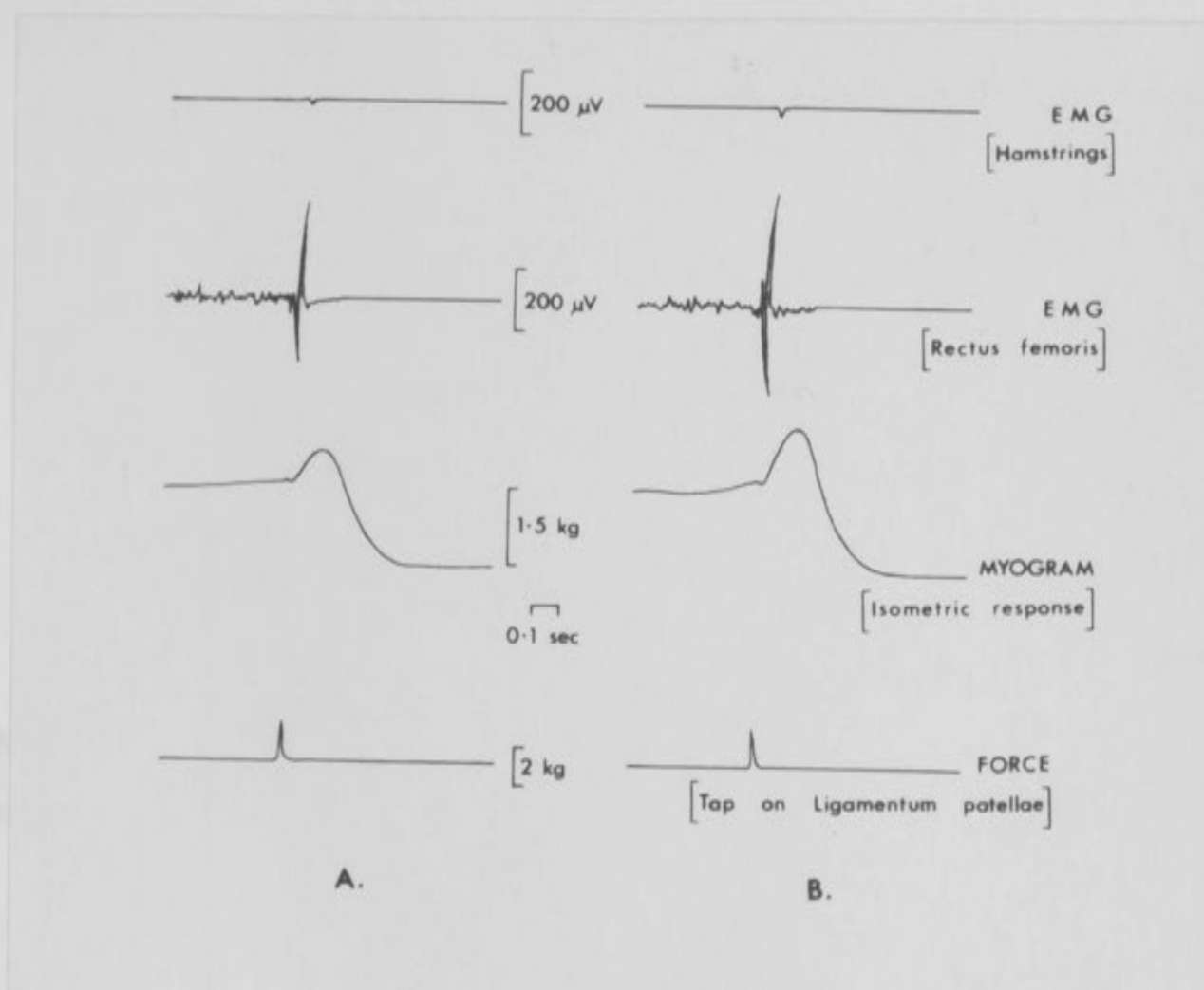


Figure 21

Electromyograms and force records of the patellar reflex during:

- (A) pre-strain of $1\frac{1}{2}$ kg force at the ankle cuff before the tap on the ligament and
- (B) pre-strain of $1\frac{1}{2}$ kg with a concurrently executed JM (1 sec) before the tap on the ligament.

Subject B.H.

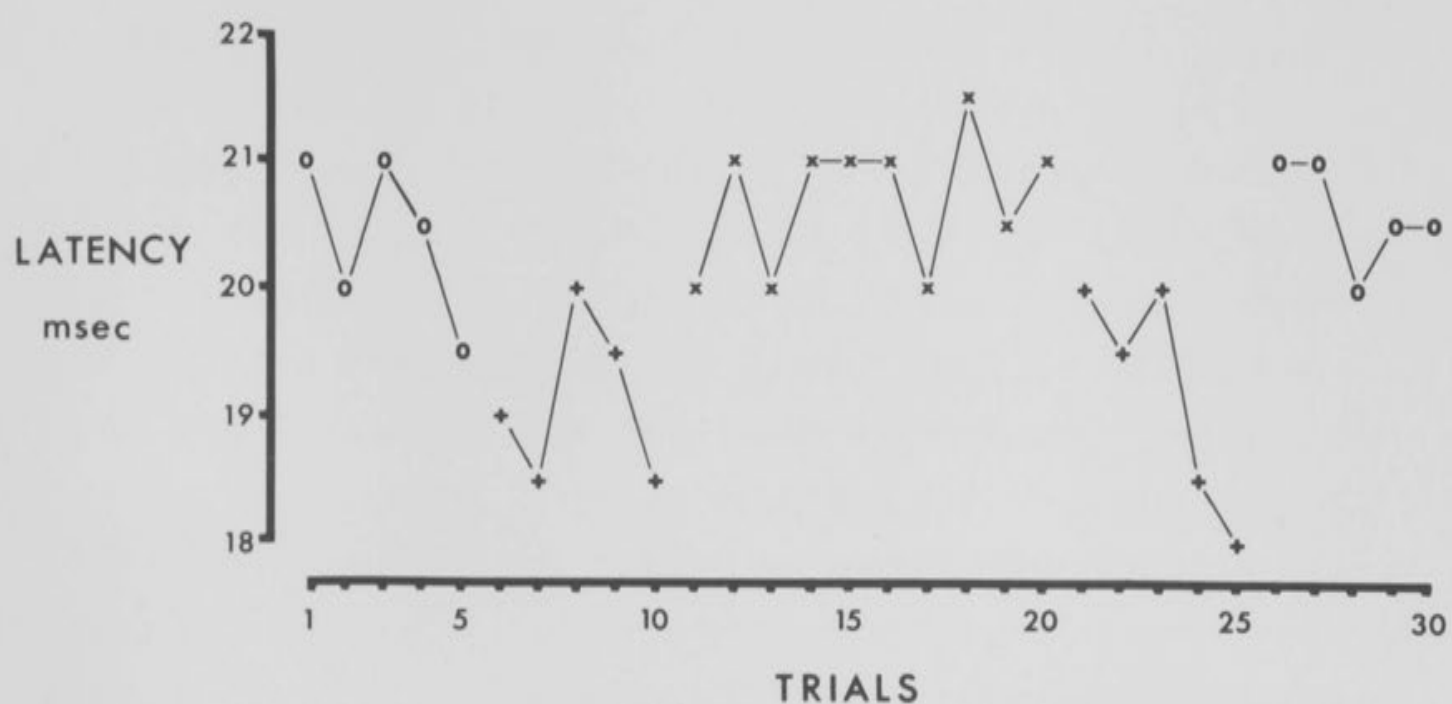


Figure 22

Graph of the data from a counterbalanced experimental design to show the decrease in latency ($p < 0.001$) for the patellar reflex during JM (1 sec) trials (+) compared with control trials (o), while JM (10 sec) trials (x) are not dissimilar from control (Student's $t = 0.89$, $df = 18$). Subject B.H.

Correlation coefficients

The two types of JM had no marked effect on the magnitude of the product-moment correlation coefficients between the electrical and mechanical responses (Table VIII).

DISCUSSION

The results of these experiments confirm previous evidence for the strong facilitation of the motoneurons supplying the extensor muscle in a phasic stretch reflex when a JM is executed briefly before the tap on the ligament (Varnum, 1934; Buller and Dornharst, 1957; Paillard, 1959; Benson and Gedye, 1961; Rabending and Koch, 1962). The fact that the force of the tap used to elicit the reflex has to be reduced by approximately 760 g during JM (1 sec) treatment in order to match the size of the control responses, indicates the powerful facilitatory effect of this experimental treatment. Augmentation was found within a range of muscle tonus (provided tonus was consistent between treatments within a session) from normal resting tension to $1\frac{1}{2}$ kg pre-strain, measured at the ankle. Prolonged execution of the JM or the absorption of an inter-neuronal blocking agent resulted in the loss of augmentation.

These differential effects cannot be attributed to peripheral influences such as alteration in muscle length as a result of change in muscle tone. The pendulum-hammer was released from a uniform height within sessions and no significant difference existed

between the mean peak force on the ligament between control and experimental treatments. Therefore, it may be assumed that the rate and amount of extension of extrafusal fibres was similar from trial to trial and no change in the frequency of discharge or in the number of muscle stretch receptors responding could occur without central influence.

The loss of augmentation during the JM (10 sec) treatment cannot be the result of muscle fatigue because no progressive reduction in response was observed for any S over the ten experimental trials. In fact, some Ss gave slightly larger responses towards the end of the set of experimental trials than at the beginning.

Under normal experimental conditions, a generalised arousal of reticular neurones probably occurs when a JM initially is begun and this results in the raised excitability of alpha and gamma motoneurones. Continued execution of the JM presumably results in adaptation of reticular neurones so that descending impulses are attenuated; in these circumstances alpha and gamma motoneurones display no more excitability than is usual during relaxed conditions. The separate effects of direct and indirect descending pathways may be distinguished in the pre-strain experiments. It may be assumed that the influence of the fusimotor regulation of spindle sensitivity is removed to a substantial degree and since a briefly executed JM still augments the reflex, direct facilitation of alpha motoneurones

seems a reasonable assumption. In the drug experiments, the inhibitory action of Myanesin on polysynaptic pathways in the spinal cord would reduce both the direct action on the alpha motoneurones and the indirect fusimotor sensitisation of the spindles. The lack of augmentation of the reflex during the JM (1 sec) under the peak drug effect seems to confirm this assumption.

Analysis of the data dealing with the variance of the reflex responses (as a probable index of fusimotor activity) lends support to the propositions put forward. When experimental manipulations do not interfere with fusimotor regulation of the spindles, JM (1 sec) conditions presumably activate the fusimotor system with consequent increased variance of the reflex responses. On the other hand, JM (10 sec) conditions would be expected to result in adaptation of the fusimotor system so that reflex responses would be no different in variance from control responses. The results confirm these predictions (Table VIII). Unloading the spindles during pre-strain trials, thus attenuating fusimotor influence, resulted in no increase in variance during the JM (Table X). Likewise, the variance of control and JM responses during fusimotor blockade by Myanesin was not dissimilar (Table IX). Generally, there was an increase in the variance of reflex responses compared with control when fusimotor activity was thought to be exerting a pronounced effect on spindle sensitivity whilst there was no change in the variance when fusimotor activity was attenuated.

Further indications of fusimotor effects may be found in latency records because biasing causes the spindle to become a more sensitive and faster responding receptor (Homma, et al., 1962) without any detectable change occurring in extrafusal tension (Eldred and Fujimori, 1958). Evidence from human experiments has shown a reduction in the latency of the knee-jerk during physical activity in remote muscles (Golla and Hettwer, 1923; Varnum, 1934), and, under these circumstances, fusimotor biasing of the spindles may be assumed. The present experiments confirm that when fusimotor influence may be assumed [that is, in JM (1 sec) trials for normal, pre-drug, post-drug ($1\frac{1}{2}$ h) and all placebo trials], there is a significant reduction in latency. Whereas, when descending pathways may be assumed to be blocked [that is, in post-drug ($\frac{1}{2}$ h) trials], or when fusimotor discharge is assumed to be attenuated [that is, in JM (10 sec) trials], no change in latency is observed (Table VIII and Figure 22). Unfortunately, the method used did not permit latency to be measured during pre-strain trials because asynchronous MAPs during active contraction triggered the timer before the synchronous MAP of the reflex occurred. The prediction, under pre-strain treatment, being that no change in latency would be observed in JM (1 sec) trials compared with control trials.

The general findings in this set of experiments confirm the proposition that increased mean and variance of responses together with decreased latency

are reliable indices of fusimotor sensitisation of muscle spindles.

The results of these experiments support the findings of Landau and Clare (1964) who concluded that it was not necessary to postulate that the JM augments the stretch reflex specifically by way of the fusimotor system. Apparently spindle biasing is not the sole facilitatory mechanism for the reflex; direct action on the alpha motoneurons by supra-spinal influences seems to play a part.

The data also show that under both of the JM treatments, correlation coefficients between electrical and mechanical responses remain high. Apparently, increased supra-spinal influence does not affect the linearity of the relationship between the impulse of the MAP and the impulse of the isometric contraction provided muscle tonus and muscle length remain unaltered.

Implications for the experiment

The probable reasons for this result are as follows. The spindles lie 'in parallel' with the extrafusal fibres so that, since during isometric contractions the elasticity of the tendon permits some shortening of the extrafusal fibres (Lunt and Kuffler, 1951; Kilduff, et al., 1953; Gross, 1955a), the spindles become unloaded. When this happens facilitatory discharges begin to adjust the length of the intrafusal fibres to the new length of the extrafusal fibres in order that information about the state of the muscle will continue to flow to the CNS. However, there is a time delay in this operation because the

CHAPTER X

THE EFFECT OF PRE-STRAIN IN THE RESPONDING MUSCLE
ON THE PATELLAR REFLEX

The results of previous experiments in this programme have shown that increased variance of the responses seems to be a reliable index of fusimotor biasing of the muscle spindle. The results of the pre-strain trials in the JM experiments described in Chapter IX, showed that there was a significantly smaller variance in pre-strain trials compared with control (zero pre-strain) trials (Table X). Apparently during rapid, active contraction of the muscle, gamma activity had a reduced effect on spindle sensitivity.

Rationale for the experiment

The probable reasons for this result are as follows. The spindles lie 'in parallel' with the extrafusal fibres so that, since during isometric contractions, the elasticity of the tendons permits some shortening of the extrafusal fibres (Hunt and Kuffler, 1951; Eldred, et al., 1953; Granit, 1955a), the spindles become unloaded. When this happens fusimotor discharges begin to adjust the length of the intrafusal fibres to the new length of the extrafusal fibres in order that information about the state of the muscle will continue to flow to the CNS. However, there is a time delay in this operation because the

excitation of motor end-plates on the intrafusal fibres occurs by way of small diameter, slow conducting, gamma fibres. In human limb muscles the time lag may be about 40 msec (Merton, 1953). Therefore, in a rapidly contracting muscle it seems reasonable to assume that gamma biasing of the spindles would be attenuated considerably. In fact, experimental evidence from animal studies has shown that spindle responses to fusimotor stimulation are greatly reduced by concomitant extrafusal contraction (Hunt and Perl, 1960).

The pre-strain technique thus provides a favourable experimental method for reducing fusimotor biasing below control level. The method also provides a situation for testing the proposition put forward in Chapter IV that consistent muscle tonus is an important variable contributing to the linear relationship between the mechanical and electrical responses in the phasic stretch reflex. That is, various levels of active contraction of the rectus femoris muscle may be investigated and compared with normal resting tension.

The aims of the experiment were to find out whether:

- (a) the impulse of the isometric contraction is related to the impulse of the MAP under conditions of known pre-strain exerted by the rectus femoris muscle in a phasic stretch reflex (the patellar reflex).

- (b) A decrease in the variance of the responses occurs during pre-strain conditions compared with control conditions, and
- (c) the height (maximum force of the isometric contraction) and area (impulse of the isometric contraction) of the myogram response bear a high, positive relationship under pre-strain conditions as well as under control conditions.

The expectations were that the effects of pre-strain on the reflex responses would be differential. The greater the pre-strain, the greater the tension in the muscle. Consequently, the more shortening of the muscle and unloading of the spindles; therefore the smaller the variance of the responses. Also, if the responses under control and pre-strain conditions were pooled, the correlation coefficient between the mechanical and electrical responses would be reduced below the coefficients for the various levels of muscle tension considered separately.

Subjects

Four normal adult Ss (2 males, 2 females) participated in the experiment. All had been Ss in previous experiments and were well trained in relaxation.

Apparatus and method

The apparatus used was similar to that previously described except that, in addition, a meter was connected to the output of the pen recorder so that the S could observe the response from a transducer-load cell unit which was linked to the ankle cuff for isometric recording. By observing the meter response, the Ss could exert the required pre-strain (1/2 kg, 1 kg and 1 1/2 kg) before the ligament was tapped mechanically to elicit the reflex. The Ss were instructed to report as soon as the meter needle reached the required reading and the E then released the pendulum-hammer. On feeling the tap on the ligament, the Ss relaxed the active contraction of the rectus femoris muscle to permit the stretch reflex to occur with subsequent decay of the myogram to zero. A screen prevented the S observing the fall of the hammer.

Figure 23 shows how the impulse of the isometric reflex contraction (that is, the net reflex component from a given pre-strain value) was determined by subtracting the voluntary relaxation component from the gross myographic response. The control responses and gross pre-strain responses were obtained by tapping the ligament whereas the myogram of voluntary relaxation was obtained by lightly tapping the tubercle of the tibia. The minute tap on the ligament was used (a) to avoid eliciting an involuntary response and (b) as a signal for the S to relax so that the latency of the voluntary response could be calculated.

Reflex responses which did not meet the following criteria were discarded:

- (a) di-phasic MAP without obvious repetitive activity in rectus femoris
- (b) negligible activity in the hamstring EMG, and
- (c) a smooth decay from peak force to zero in the myogram.

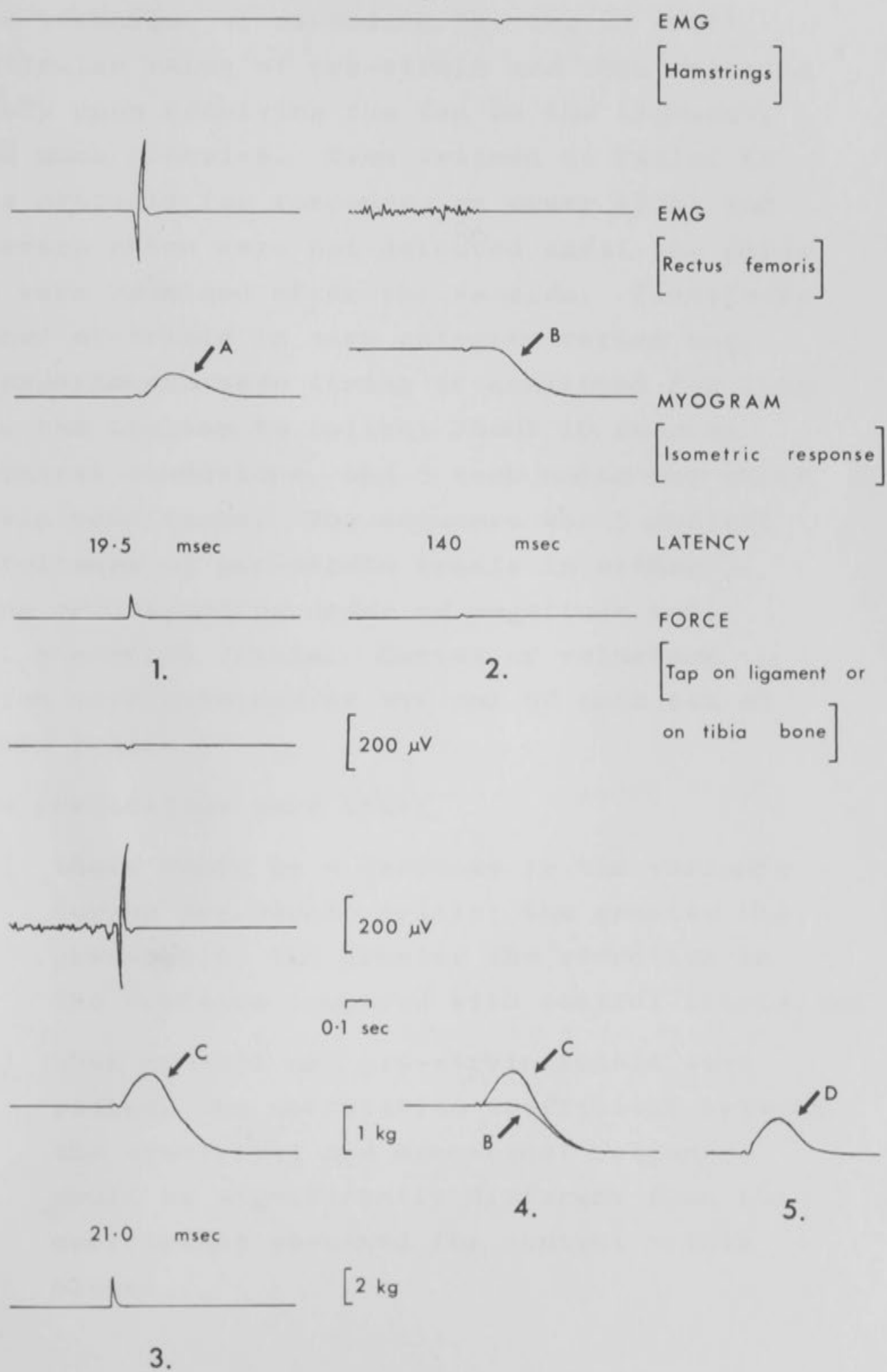
Latency measures were made for control trials but the asynchronous MAPs during voluntary contraction usually triggered the timer beforehand during pre-strain trials. The latency for voluntary relaxation trials was measured, approximately, from the paper records (Figure 23).

Figure 23

EMG, myogram latency and force records of the isometric response to (1) a tap on the ligamentum patellae to show a control (zero pre-strain) response, (2) a light tap on the tubercle of the tibia to show the myogram of voluntary relaxation from 1 kg pre-strain, (3) a tap on the ligamentum patellae to show an involuntary response from 1 kg pre-strain.

The drawing at 4 shows how the area of the reflex component of the myographic response at 3 was determined by superimposing the curves B and C. The curve D in the drawing 5 shows the area of the reflex component constructed on a horizontal base-line. The shapes at A and D are similar. The EMGs from the hamstring muscle show negligible activity throughout. Subject B.H.

FIGURE 23



Experimental design

The technique of extending the leg to exert the particular value of pre-strain and then relaxing completely upon receiving the tap on the ligament, required much practice. Even trained Ss failed to meet the criteria for responses on every trial and small errors often were not detected until the paper records were examined after the session. Therefore, the number of trials in each category varied but, as the experiments were tiring if continued for long periods, the aim was to collect about 10 records under control conditions, and 5 each under the three pre-strain conditions. The sequence was 5 control trials followed by pre-strain trials in either ascending or descending order of magnitude and, finally, 5 control trials. Curves of voluntary relaxation were obtained at the end of each set of pre-strain trials.

The predictions were that:

- (i) there would be a decrease in the variance during pre-strain trials; the greater the pre-strain, the greater the reduction in the variance compared with control trials, and
- (ii) when control and pre-strain trials were pooled, the correlation coefficient between the electrical and mechanical responses would be significantly different from the coefficient obtained for control trials alone.

The difference between the means for each treatment was observed to find out what changes occurred but as the muscle tonus varied between treatments, no firm conclusions could be made about the results.

RESULTS

Independent variable

The pendulum-hammer used to elicit the reflex was released from uniform height within sessions. Therefore, when muscle tone was altered during the various pre-strain conditions, the increased resistance offered by the ligament to the hammer depressing it, resulted in larger forces being recorded by the strain-gauge mounted in the hammer head. Table XI gives data to show the magnitude of the forces involved, the pre-strain forces being significantly greater than those for control trials.

Comparison of the variances

Whilst there was general evidence for a decrease in the variance of the responses with increased pre-strain, there were some exceptions to this finding, for example, W.R. in session 1 and B.H. in session 4. Also, the decrease in the variance was not always significantly different from that during control trials, for example, B.H. in session 3 (Table XI).

The results for the mathematical responses (impulse of the isometric contraction) and electrical responses (impulse of the MAP) were similar (Table XI).

Figures 24, 25 and 26 illustrate the reduction in variability during pre-strain trials compared with

TABLE XI
DATA RELEVANT TO THE INDEPENDENT VARIABLE (PEAK FORCE OF TAP ON THE LIGAMENTUM PATELLAE) AND DEPENDENT VARIABLES (IMPULSE OF ISOMETRIC REFLEX CONTRACTION AND IMPULSE OF MUSCLE ACTION POTENTIAL) FOR CONTROL AND PRE-STRAIN TREATMENTS.

| Subject | Treatment | N | Peak Force on Ligament (kg) | | | Impulse of Isometric Contraction (g sec) | | | | Impulse of Muscle Action Potential (μ V sec) | | | | PRODUCT-MOMENT CORRELATION | | | |
|--------------------|--------------------|------|-----------------------------|---------|---------|--|---------|----------------|------|---|--------|----------------|-------|----------------------------|----------------|-----------------|-------|
| | | | \bar{X} | t | | \bar{X} | t | S ² | F | \bar{X} | t | S ² | F | r | t ⁺ | z ^{**} | r |
| A.M. | Control | 7 | 1.83 | | 186.3 | | 3194.0 | | 1.11 | | 0.14 | | 0.942 | | | | 0.990 |
| | Pre-strain | 10 | 2.09 | 9.06*** | 150.4 | 1.32 | 2879.0 | 1.10 | 1.66 | 2.64* | 0.19 | 1.38 | 0.942 | 0.00 | 0.87 | | 0.763 |
| | Total | 17 | | | | | | | | | | | 0.578 | | 1.97* | | |
| | Control | 6 | 2.01 | | 126.0 | | 10237 | | 0.63 | | 0.69 | | 0.946 | | | | 0.981 |
| | Pre-strain | 5 | 2.13 | 1.28 | 70.8 | 1.29 | 703.46 | 14.5* | 0.65 | 0.06 | 0.05 | 13.9* | 0.816 | 0.91 | 0.27 | | 0.990 |
| | Total | 11 | | | | | | | | | | | 0.879 | | 0.68 | | |
| | Control | 15 | 1.82 | | 282.5 | | 7669.3 | | 1.05 | | 0.27 | | 0.963 | | | | 0.973 |
| | 1/2kg pre-strain | 8 | 2.03 | 5.09*** | 197.0 | 3.22** | 4523.0 | 1.69 | 1.20 | 0.75 | 0.18 | 1.48 | 0.969 | 0.10 | 0.27 | | 0.998 |
| | 1kg pre-strain | 8 | 2.11 | 7.25*** | 123.3 | 5.75*** | 2055.9 | 3.73* | 1.06 | 0.83 | 0.05 | 5.09* | 0.935 | 0.64 | 0.30 | | 0.989 |
| 1 1/2kg pre-strain | 10 | 2.09 | 5.49*** | 86.8 | 7.69*** | 1302.6 | 5.89** | 0.96 | 0.54 | 0.06 | 4.23* | 0.854 | 1.18 | 1.47 | | 0.987 | |
| Total | 41 | | | | | | | | | | | 0.656 | | 3.59*** | | | |
| V.H. | Control | 7 | 2.05 | | 41.7 | | 618.8 | | 0.75 | | 0.11 | | 0.859 | | | | 0.984 |
| | Pre-strain | 6 | 2.05 | 0.06 | 69.3 | 1.48 | 1720.0 | 2.78 | 2.64 | 8.49*** | 0.23 | 2.16 | 0.937 | 0.66 | 0.58 | | 0.899 |
| | Total | 13 | | | | | | | | | | | 0.683 | | 0.77 | | |
| | Control | 7 | 2.36 | | 68.0 | | 4075.4 | | 0.38 | | 0.06 | | 0.974 | | | | 0.955 |
| | 1/2kg pre-strain | 7 | 2.49 | 3.07** | 166.9 | 3.10** | 3075.3 | 1.33 | 1.15 | 5.09*** | 0.10 | 1.68 | 0.958 | 1.20 | 0.20 | | 0.998 |
| | 1kg pre-strain | 7 | 2.68 | 7.55*** | 157.7 | 3.10** | 1777.6 | 2.29 | 1.28 | 6.41*** | 0.08 | 1.29 | 0.783 | 1.88 | 1.49 | | 0.879 |
| | 1 1/2kg pre-strain | 7 | 2.72 | 6.39*** | 91.4 | 0.94 | 229.4 | 17.8** | 1.09 | 6.46*** | 0.02 | 2.45 | 0.549 | 0.90 | 2.08* | | 0.844 |
| | Total | 28 | | | | | | | | | | | 0.812 | | 1.93* | | |
| | Control | 10 | 1.69 | | 88.2 | | 4638.0 | | 1.55 | | 1.20 | | 0.978 | | | | 0.998 |
| 1/2kg pre-strain | 5 | 2.02 | 8.49*** | 107.6 | 0.24 | 866.2 | 5.36 | 2.21 | 1.29 | 0.11 | 11.0* | 0.934 | 1.38 | 0.70 | | 0.953 | |
| 1kg pre-strain | 6 | 2.25 | 15.6*** | 74.7 | 0.12 | 981.3 | 4.73* | 1.73 | 0.36 | 0.13 | 8.96* | 0.829 | 0.61 | 1.54 | | 0.807 | |
| 1 1/2kg pre-strain | 8 | 2.46 | 21.0*** | 92.8 | 0.18 | 536.9 | 8.64** | 1.65 | 0.25 | 0.06 | 21.4** | 0.779 | 0.77 | 2.06 | | 0.877 | |
| Total | 29 | | | | | | | | | | | 0.933 | | 1.34 | | | |
| B.H. | Control | 10 | 1.36 | | 128.4 | | 5082.2 | | 3.68 | | 2.74 | | 0.993 | | | | 0.996 |
| | 1/2kg pre-strain | 5 | 1.59 | 2.84* | 106.4 | 0.63 | 1589.5 | 3.20 | 3.97 | 0.36 | 0.65 | 4.20 | 0.947 | 0.80 | 1.28 | | 0.986 |
| | 1kg pre-strain | 5 | 1.72 | 4.31*** | 130.0 | 0.05 | 230.4 | 22.1** | 4.57 | 1.13 | 0.34 | 8.05* | 0.937 | 2.07 | 1.39 | | 0.984 |
| | 1 1/2kg pre-strain | 5 | 1.71 | 3.99** | 136.4 | 0.23 | 709.5 | 7.17* | 3.74 | 0.08 | 0.58 | 4.75 | 0.896 | 1.30 | 1.72 | | 0.974 |
| | Total | 25 | | | | | | | | | | | 0.913 | | 2.94** | | |
| | Control | 10 | 1.61 | | 151.0 | | 1487.4 | | 4.66 | | 1.47 | | 0.931 | | | | 0.977 |
| | 1/2kg pre-strain | 6 | 1.86 | 6.27*** | 194.7 | 2.27* | 1178.8 | 1.26 | 6.96 | 3.36** | 2.33 | 1.58 | 0.938 | 0.53 | 0.08 | | 0.971 |
| | 1kg pre-strain | 6 | 1.91 | 7.03*** | 149.7 | 0.05 | 2832.5 | 1.90 | 6.16 | 2.06 | 3.08 | 2.09 | 0.957 | 0.03 | 0.36 | | 0.994 |
| | 1 1/2kg pre-strain | 6 | 2.07 | 9.96*** | 117.0 | 1.61 | 1465.0 | 1.02 | 5.68 | 1.58 | 1.73 | 1.17 | 0.916 | 0.16 | 0.15 | | 0.966 |
| | Total | 28 | | | | | | | | | | | 0.818 | | 1.20 | | |
| | Control | 10 | 1.70 | | 209.2 | | 12803.4 | | 3.32 | | 2.56 | | 0.979 | | | | 0.999 |
| | 1/2kg pre-strain | 5 | 1.76 | 1.62 | 177.6 | 0.59 | 650.2 | 19.7** | 2.92 | 0.52 | 0.71 | 3.62 | 0.974 | 3.20** | 0.13 | | 0.989 |
| | 1kg pre-strain | 5 | 2.04 | 5.66*** | 130.8 | 1.48 | 388.2 | 32.9*** | 2.51 | 1.07 | 0.09 | 26.4** | 0.657 | 0.17 | 1.85 | | 0.985 |
| | 1 1/2kg pre-strain | 5 | 2.12 | 4.56*** | 155.6 | 1.00 | 1006.0 | 12.7* | 3.08 | 0.31 | 0.19 | 13.4* | 0.927 | 0.06 | 0.79 | | 0.959 |
| | Total | 25 | | | | | | | | | | | 0.927 | | 1.50 | | |
| L.V. | Control | 12 | | | 200.5 | | 1321.4 | | 1.53 | | 0.17 | | 0.949 | | | | 0.926 |
| | 1/2kg pre-strain | 5 | not available | | 176.4 | 0.85 | 3434.2 | 2.59 | 1.55 | 0.07 | 0.24 | 1.45 | 0.977 | 1.10 | 0.59 | | 0.999 |
| | 1kg pre-strain | 8 | | | 73.8 | 9.50*** | 526.4 | 2.51 | 0.76 | 6.04*** | 0.02 | 6.75** | 0.929 | 0.72 | 0.31 | | 0.911 |
| | 1 1/2kg pre-strain | 4 | | | 27.5 | 8.44*** | 134.8 | 9.79* | 0.55 | 3.39** | 0.03 | 5.85 | 0.945 | 0.53 | 0.01 | | 0.922 |
| | Total | 29 | | | | | | | | | | | 0.946 | | 0.08 | | |
| | Control | 6 | 1.83 | | 320.0 | | 30358 | | 3.17 | | 2.35 | | 0.979 | | | | 0.995 |
| | 1/2kg pre-strain | 5 | 2.04 | 5.17*** | 212.8 | 1.31 | 2418.6 | 12.55* | 2.32 | 1.16 | 0.29 | 7.92* | 0.934 | 0.79 | 0.63 | | 0.988 |
| | 1kg pre-strain | 5 | 2.07 | 5.83*** | 98.4 | 2.71* | 2066.2 | 14.69* | 1.52 | 2.27 | 0.21 | 10.9* | 0.991 | 0.38 | 0.46 | | 0.999 |
| | 1 1/2kg pre-strain | 5 | 1.95 | 3.12* | 146.0 | 2.17 | 464.0 | 65.4** | 1.96 | 1.69 | 0.11 | 22.4** | 0.956 | 0.98 | 0.41 | | 0.948 |
| | Total | 21 | | | | | | | | | | | 0.977 | | 0.07 | | |
| | Control | 10 | 1.82 | | 317.6 | | 11924.6 | | 0.97 | | 0.25 | | 0.941 | | | | 0.987 |
| | 1/2kg pre-strain | 5 | 1.91 | 2.67* | 212.8 | 1.78 | 1834.6 | 6.49* | 0.70 | 1.15 | 0.01 | 41.3*** | 0.778 | 0.82 | 0.88 | | 0.995 |
| | 1kg pre-strain | 5 | 2.18 | 10.4*** | 97.6 | 4.26*** | 1049.4 | 11.4* | 0.37 | 2.55* | 0.01 | 25.4*** | 0.856 | 0.36 | 0.57 | | 0.974 |
| | 1 1/2kg pre-strain | 5 | 2.27 | 13.0*** | 92.4 | 13.9*** | 227.8 | 52.3*** | 0.39 | 2.46* | 0.01 | 48.4*** | 0.979 | 0.02 | 0.66 | | 0.978 |
| | Total | 25 | | | | | | | | | | | 0.932 | | 0.17 | | |

Probability levels: *P < 0.05, **P < 0.01, ***P < 0.001 (All comparisons with control measures).

+ Two-tailed t-test of difference between slope of regression lines.

** Z test of difference between correlation coefficients.

... was reduced significantly compared with the coefficient for control trials in only 4/12 sessions (Table XI).

The results for the mechanical responses (impulse of the isometric contraction) and electrical responses (impulse of the MAP) were similar (Table XI).

Figures 24, 25 and 26 illustrate the reduction in variance during pre-strain trials compared with control trials.

Product-moment correlations

High, positive correlation coefficients were found between mechanical and electrical responses within treatments. With one exception (W.R. in session 2) no coefficient during separate pre-strain treatments was significantly different from the control coefficient within sessions on a two-tailed Z test between correlation coefficients (Table XI).

However, three correlation coefficients during pre-strain treatment were not significantly different from zero. These were:

| Subject | Session | r | df | <u>t</u> | P |
|---------|---------|-------|----|----------|--------|
| A.M. | 2 | 0.816 | 3 | 2.48 | < 0.10 |
| W.R. | 2 | 0.549 | 5 | 1.47 | < 0.50 |
| B.H. | 4 | 0.657 | 3 | 1.55 | < 0.50 |

Without exception, the correlation coefficient for combined control and pre-strain trials was smaller than the coefficient for control trials. However, one-tailed Z tests showed that the coefficient for combined trials was reduced significantly compared with the coefficient for control trials in only 4/12 sessions (Table XI).

Figure 24

Graph to show the relationship between the impulse of the isometric contraction and the impulse of the MAP during pre-strain trials early in the training period. The pre-strain responses for all values fall along a single regression line and there is a decrease in variance during experimental trials compared with control trials. Subject B.H.

Figure 25

Graph to show the relationship between the impulse of the isometric contraction and the impulse of the MAP during pre-strain trials after some training. There are separate regression lines for control and pre-strain trials and the slopes of these lines are not dissimilar. Subject A.M.

Figure 26

Graph to show the relationship between the impulse of the isometric contraction and the impulse of the MAP during pre-strain trials for a highly trained S. There is a separate regression line (the slopes of which are not dissimilar) for control and each value of pre-strain. Subject A.M.

FIGURE 24

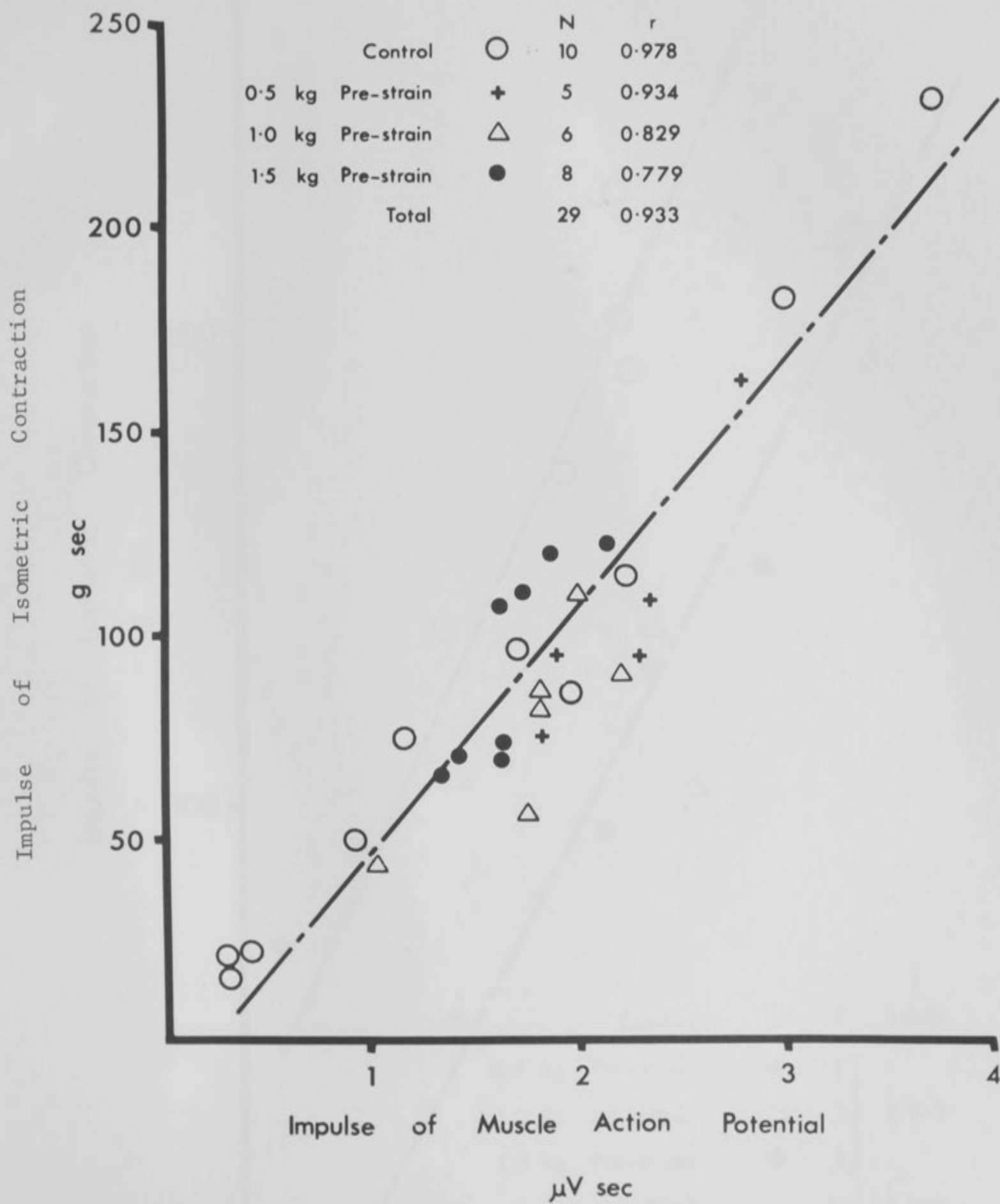


FIGURE 25

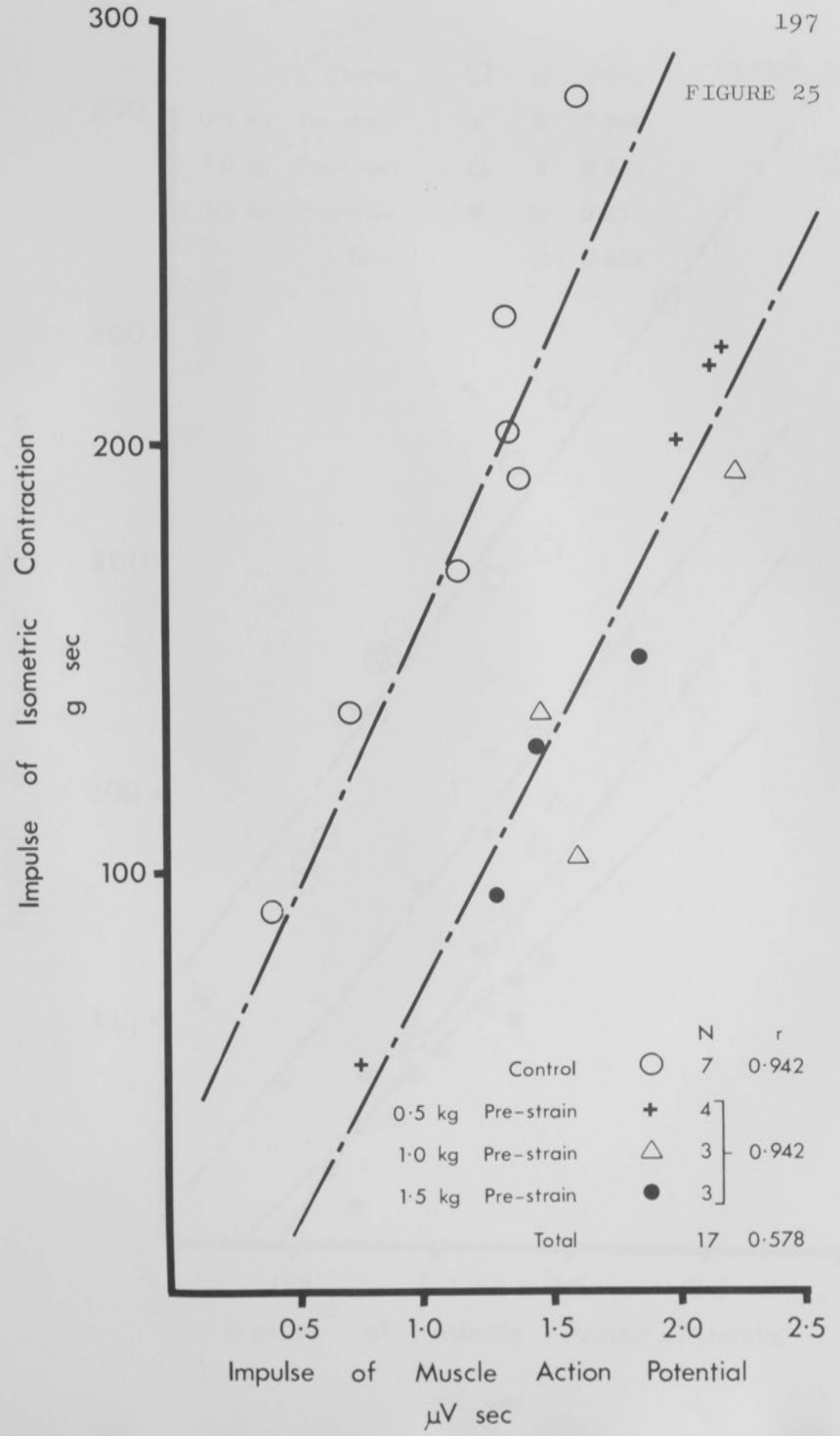
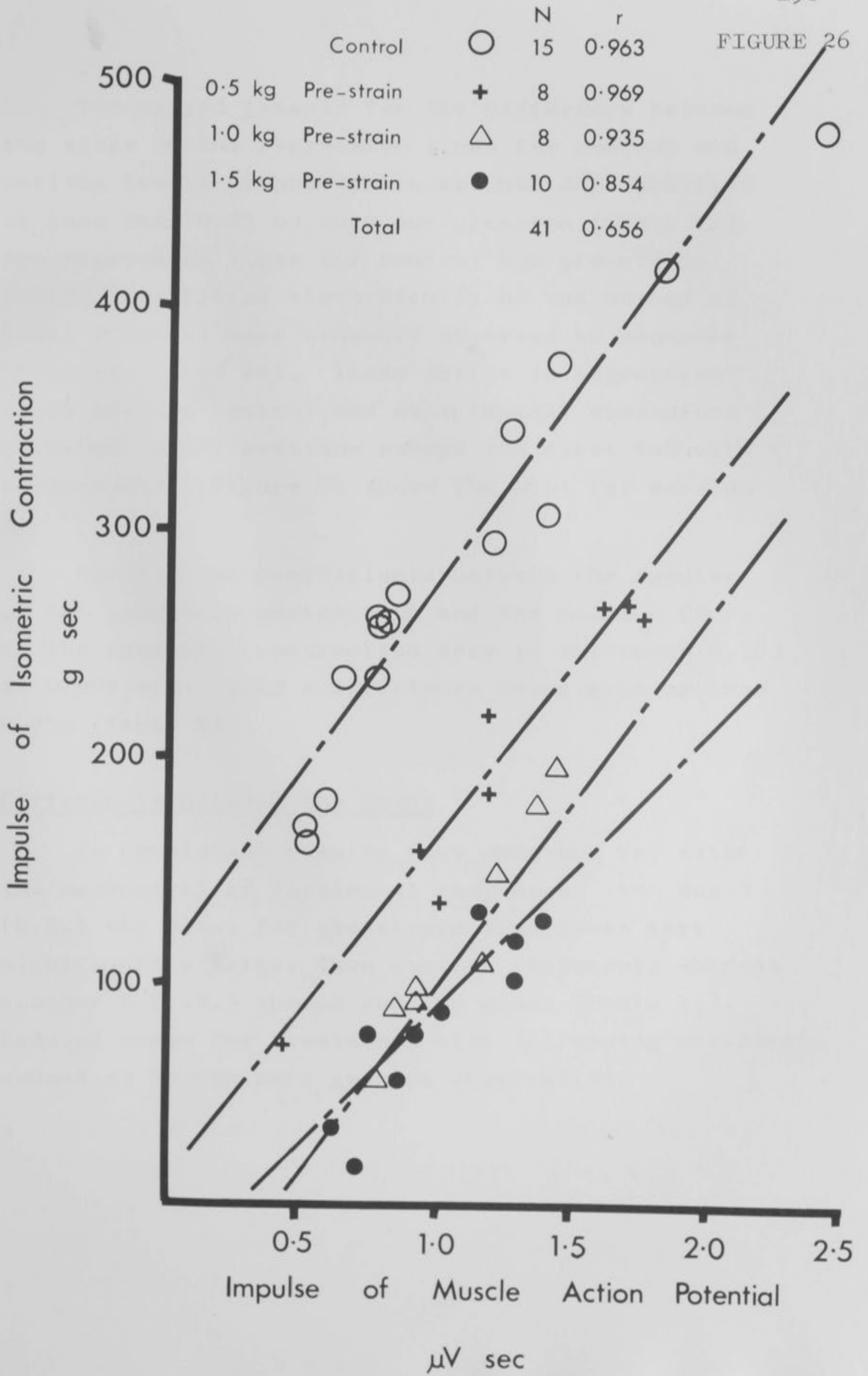


FIGURE 26



Two-tailed t -tests for the difference between the slope of the regression lines for control and various levels of pre-strain reached a probability of less than 0.05 on only one occasion (Table XI). The regression lines for control and pre-strain (which were fitted algebraically by the method of least squares) were commonly observed to separate (Figures 25 and 26). These shifts in regression lines between control and experimental treatments occurred in all sessions except the first two with subject B.H. (Figure 24 shows the plot for session 1).

Correlation coefficients between the impulse of the isometric contraction and the maximum force of the isometric contraction were in the range 0.763 to 0.999 with 32/42 coefficients being greater than 0.950 (Table XI).

Differences between the means

No consistent results were obtained for either the mechanical or electrical responses. For one S (W.R.) the means for pre-strain treatments were significantly larger than control responses, whereas another S (L.V.) showed reduced means (Table XI). Reduced means for treatments with increasing pre-strain seemed to be the more general observation.

DISCUSSION

The variance as an index of fusimotor biasing of the spindles

This experiment provides further evidence for the view that a reliable index of fusimotor sensitisation of muscle spindles may be obtained from the variance of the responses in the patellar reflex. In general, there was a progressive decrease in the variance with an increase in pre-strain level which is consistent with the assumption that rapid, active contraction of the muscle unloads the spindles. In this circumstance, the effect of fusimotor activity is considerably reduced. It seems that under the conditions of this experiment, the reflex was elicited before the gamma impulses could adjust the intrafusal fibres to the length of the extrafusal fibres.

The decrease in the variance cannot be explained in terms of the reduced range of responses imposed upon the muscle by the pre-strain treatment. For example, it could be assumed that most ventral horn cells were engaged in the voluntary contraction of the muscle and only a limited number of cells were available for the additional reflex contraction when the ligament was tapped. The tension in the rectus femoris muscle during a pre-strain of $1\frac{1}{2}$ kg recorded at the ankle cuff was approximately $7\frac{1}{2}$ kg (calculated by the torque formula $Fd = F_1d_1$). However, despite this large tension, it was possible to augment the muscle response significantly by a JM as described in Chapter IX. Therefore, an explanation of a decrease

in the variance because of the physical limitation placed on the responses is not tenable.

The few latency measures which were possible during pre-strain trials lend support to the view that fusimotor regulation of spindle sensitivity was minimised during this treatment. The EMG potentials during an active contraction triggered the timer before the spike of the MAP occurred during the reflex and only one or two observations were made during each session. These were inadequate to permit a statistical analysis to be made and, therefore, the evidence is slender but an increase in latency seems to occur during pre-strain trials (Figure 23). Previous experiments have shown that a decrease in latency is associated with indications of fusimotor biasing. This is because biasing makes the receptor a more sensitive and much faster organ; it would be reasonable to assume the converse when fusimotor biasing is largely attenuated.

Changes in muscle tonus

There is no doubt that muscle tonus altered between control and pre-strain treatments because the S extended the leg during pre-strain trials at forces of $\frac{1}{2}$, 1 and $1\frac{1}{2}$ kg. Also, the forces registered by the strain gauge in the head of the hammer, without exception, were significantly greater during pre-strain trials than during control trials. In general, there was a progressive increase in force on the ligament with increase in pre-strain.

The changes in muscle tonus seem to have the effect of altering the level of response sensitivity in such a way that for any given mechanical response, the electrical response increases with increased muscle tonus (Figures 25 and 26). Conversely, for any given electrical response, the mechanical response decreases with increased muscle tonus. The systematic shift in response sensitivity is shown by the progressive sequence of the mathematically fitted regression lines (which are not dissimilar in slope) with increased pre-strain (Table XI and Figures 25 and 26).

This finding also indicates that constancy of the tension in the muscle is necessary in order to obtain a high, positive relationship between the impulse of the isometric contraction and the impulse of the MAP. The shifts in response sensitivity found in the pre-strain treatments have the effect of destroying the linearity of the relationship between the mechanical and electrical responses if all trials are used in the calculation of the correlation coefficient, irrespective of the degree of muscle tension. A reduction in the size of the coefficient when all trials were grouped occurred without exception (although the reduction was not always significant).

The changes in muscle tension as well as the slight shortening of the muscle (because of the elasticity of the tendons) which occurred between treatments in this experiment precludes a comparison of the differences between means within sessions.

Correlation between height and area of the myogram

High, product-moment correlation coefficients were found within treatments between the impulse of the isometric contraction and the maximum force of the isometric contraction. The reason for this relationship during pre-strain trials seems to be similar to the explanation for zero pre-strain (control) trials. When the MAP is a di-phasic spike with no evidence of repetitive activity and the curve of relaxation is smooth, the contraction and response times are consistent, irrespective of the height of the myogram (Figure 23 shows a pre-strain response of this character). Under these circumstances, the relationship between the height and area of the myogram would be high and positive.

Apparently, within the range of muscle tonus investigated (that is, from relaxed, resting tension to approximately $7\frac{1}{2}$ kg tension in rectus femoris muscle), the force-time relations of the muscle are programmed beforehand in the patellar reflex.

CHAPTER XI

CONCLUSIONS

The aims of this research programme were to investigate the psycho-physiology of the phasic stretch reflex by developing valid and reliable measures of the response and by gaining adequate control over the environmental and organismic variables which affect the response. When control was achieved, the neurophysiology of the stretch reflex was such that the interaction between central and peripheral events could be examined by using natural exteroceptive and proprioceptive stimuli, and behavioural manipulation of relevant variables in normal, intact human Ss. In this way, it was hoped to extend the knowledge of how the stretch reflex functions in human Ss.

The logistics of the programme were to attack the problems in the following order. First, to find valid and reliable measures of the reflex and to investigate the relationships between these variables. Second, to gain control over the reflex so that consistent responses could be elicited with uniform stimuli. Third, if this could be achieved then numerous avenues of exploration would be available during which the control responses could be used as a base-level for comparison with other treatments.

It would seem appropriate to discuss the conclusions in the same order, beginning with the measurement of response variables and ending with the general findings of experimental treatments and proposals for future research.

1. Measures of the reflex response and the relationships between these measures

Highly significant, positive, linear relationships were found between the mechanical and electrical aspects of the response, and between the height and area of the myogram. Therefore, any one of the three variables (impulse of the MAP, impulse of the isometric contraction, maximum force of the isometric contraction) can serve as an objective and readily quantifiable measure of the isometric response. However, the characteristics of the myogram and of the EMG give valuable information about the nature of the response and for this reason both records are desirable.

(a) The characteristics of the myogram

The linear relationship which was found between the mechanical aspects of the response resulted from a very narrow range of the temporal aspects of the myograms. That is, highly consistent response times and contraction times were found within sessions, irrespective of the height of the myogram (Chapter V). Consistent response time probably can occur only when a S is thoroughly trained in relaxation so that the myogram does not exhibit any 'hump' in its

relaxation phase brought about by rebound or clonus.

There is evidence that the responses in the present experiments most probably are twitches. The MAPs were discrete, di-phasic spikes of 0.04 sec duration without any evidence of repetitive EMG activity. Therefore, the motor volley probably was highly synchronous. Further, the contraction time of 0.1 sec observed in these experiments corresponds with the contraction time for twitches in response to a brief, single shock stimulus to motor nerves in human leg muscles (Fulton, 1955; Buller, et al., 1959; Prosser and Brown, 1961). For these reasons, the reflex responses of the Ss in the present work using mechanical stimulation, are most likely to be twitches of either units or groups of units operating in parallel and adding arithmetically. It seems that these refined responses were possible because of the lack of contamination by synergist muscle activity and the rigid control which was exercised over relevant environmental and organismic variables.

(b) The characteristics of the electromyogram

The criteria for the EMG from rectus femoris were (i) quiescence before and immediately following the MAP in response to the brief extension of the muscle by the mechanical tap on the ligament and (ii) a discrete, di- or tri-phasic MAP representing highly synchronous motor unit response under isometric

conditions. Figure 5 illustrates a di-phasic MAP in rectus femoris.

These criteria ensure that the muscle is relaxed and electrically silent before and immediately after the brief MAP and thus the motor volley is likely to be highly synchronous. Also, the record is clear and accurately quantifiable.

Again careful control over relevant environmental and organismic variables together with training in relaxation appears necessary in order to achieve these responses. Naive Ss display background activity and often tetra-phasic MAPs.

(c) The effect of fusimotor discharge on the relationship between the mechanical and electrical responses

Highly significant, positive product-moment correlations were obtained between these two variables during the initial experiment which tested the efficacy of control measures (Chapter V). These results were obtained under conditions where muscle tonus and fusimotor regulation of spindle sensitivity were consistent.

Later experiments, under conditions where muscle tonus was consistent but fusimotor discharge was varied systematically (Chapters VII, VIII and IX), showed that the linear relationship existed during experimental treatments designed to increase fusimotor sensitisation of the spindles as well as during control responses. The amount of activity in gamma

fibres appeared, therefore, to have no effect on the correlation between electrical and mechanical responses.

Even when the influence of fusimotor activity on the spindles was reduced below control level by unloading the spindles during pre-strain experiments (Chapter X), the linear relationship still existed for each level of pre-strain. However, these experiments showed that shifts were likely to occur in the regression lines for different levels of pre-strain (that is, different amounts of muscle tonus brought about by active contraction of rectus femoris) although the regression slopes were not dissimilar. Under these circumstances, if responses for control and all levels of pre-strain were combined to calculate the correlation, the coefficient invariably decreased, often significantly. Therefore, muscle tonus is an important variable contributing to the linear relationship between the electrical and mechanical isometric reflex responses. Unless muscle tonus is held constant for a set of trials, the correlation coefficient may decrease significantly so that the scatter diagram of the two variables, instead of being linear, becomes elliptical in shape.

(d) The efficacy of control measures to obtain consistent responses

Accurate comparisons between the control treatment and the various experimental treatments were not possible unless adequate control could be achieved

over the reflex response. The assumption made was that a consistent response was possible if environmental and organismic variables which were likely to affect the reflex response, were controlled (Chapter III). Therefore, sensory stimuli were reduced by conducting the experiments in a sound-proofed and air-conditioned room, and the Ss were trained in mental and physical relaxation.

The small standard deviations obtained in the dependent variables under control conditions testify to the success of the method (Tables of results, I to XI). Apparently, activity in supra-spinal centres of the nervous system, particularly in reticular nuclei, which are known to affect fusimotor discharge, was reduced to a reasonably constant level so that spindle sensitivity did not fluctuate greatly. On the other hand, when experimental treatments were applied which were designed to arouse supra-spinal regions of the CNS, a significantly increased variance of responses resulted.

Techniques have been developed in the present research programme which enable accurate control of the reflex responses to be achieved and this has permitted a range of experiments to be conducted to investigate the functioning of the stretch reflex.

2. Indices of fusimotor activity

The findings of the total experimental programme are summarised below.

| Type of Receptor Stimulated | Treatment | Condition | Dependent Variables Comparisons with Control Responses | | |
|-----------------------------|--|--|---|----------------------------------|----------------------------------|
| | | | IMPULSE OF MAP (μ V sec) | | LATENCY (msec) |
| | | | Mean | Variance | Mean |
| Exteroceptors | Skin stimulation (ipsilateral limb) | Agonist Antagonist | Increase Not Sig. | Increase Not Sig. | Decrease Not Sig. |
| | Visual stimulation (binocular) | 3 flashes 30 flashes | Increase Not Sig. | Increase Not Sig. | Decrease Not available |
| | Auditory stimulation (binaural) | 3 clicks 30 clicks 1000 cps Tone | Increase Not Sig. Not Sig. | Increase Not Sig. Not Sig. | Decrease Not Sig. Not Sig. |
| Proprioceptors | Activity in remote muscles (JM) | 1 sec 10 sec | Increase Not Sig. | Increase Not Sig. | Decrease Not Sig. |
| | JM plus Placebo JM plus Myanesin | 1 sec 1 sec | Increase Not Sig. | Increase Not Sig. | Decrease Not Sig. |
| | Pre-strain Pre-strain plus JM (1 sec) ⁺ | $\frac{1}{2}$, 1, $1\frac{1}{2}$ kg 1, $1\frac{1}{2}$ kg | * Increase | Decrease Not Sig. | Not available Not available |
| | Cerebral activity | Mental Calculation | Not Sig. | Not Sig. | Not Sig. |

* Not applicable because muscle tonus altered between treatments.

+ Comparison with the same value of pre-strain without JM (1 sec).

The results of these experiments dealing with the indices of fusimotor activity fall into three categories; those in which the experimental treatment either (i) increased, (ii) did not alter or (iii) decreased fusimotor activity.

First, the expectations were that when fusimotor activity was increased and allowed to take effect on the intrafusal fibres, the mean and variance of the responses would be increased while the latency would be decreased. The experimental treatments designed to increase gamma discharge consisted of (a) scratching the skin over the agonist muscle, (b) binocularly presenting a flashing light three times, (c) binaurally presenting three clicks and (d) having the S apply a JM (1 sec) normally and during placebo treatment. The predictions were confirmed without exception (Chapters VI, VII and IX).

Second, when fusimotor activity to the responding muscle was attenuated by using a repetitive train of stimuli, the expectation was that the mean, variance and latency of the responses would not be dissimilar from control responses. The experimental treatments designed to achieve this condition consisted of (a) scratching the skin over the antagonist muscle, (b) binocularly presenting a flashing light thirty times, (c) binaurally presenting thirty clicks, (d) having the S apply a JM (10 sec) and (e) using Myanesin to block supra-spinal influences. The predictions were confirmed without exception (Chapters VI, VII and IX).

Third, the expectation was that when the spindles were unloaded during a rapid, active contraction of the rectus femoris muscle, fusimotor activity would have a reduced effect on the response. The mean of the reflex responses under the control and experimental treatments could not be compared because muscle tonus changed between treatments, and the latency measures were not possible during pre-strain with the existing apparatus. The expectation was that the variance would be reduced during pre-strain responses and this was confirmed for three values of pre-strain (Chapter X). The assumption regarding the unloading of the spindles was tested by comparing responses during pre-strain with responses during pre-strain plus a concurrently executed JM (1 sec). The variances were not dissimilar and the mean increase in responses during pre-strain plus JM (1 sec) was attributed to direct supra-spinal action on the alpha motoneurons (Chapter X).

In the two other experiments (1000 cps tone and mental activity) the stimulation apparently did not arouse the gamma system sufficiently to show significant effects. In these two cases the three indices of fusimotor activity during the experimental treatments were not significantly different from control.

The finding that augmentation was possible during the pre-strain plus JM (1 sec) treatment compared with ordinary pre-strain seems to indicate that a significantly increased mean response does not alone

reflect fusimotor biasing of the spindles. Augmentation apparently is the result of a compounding of direct and indirect supra-spinal influences and therefore is not a pure index of increased fusimotor activity. However, when increased mean response, increased variance and decreased latency were observed together, they have been shown to be highly reliable indices of increased fusimotor activity.

This conclusion is entirely consistent with the findings of experiments with infra-human animals conducted by neurophysiologists. These points have been discussed in detail in previous chapters but are briefly listed again. Gamma biasing makes the spindle a much more sensitive and faster responding receptor so that there is an increase in its discharge from the primary ending when the muscle is stretched and the spindle is extended. This results in a greater extrafusal response and a decrease in reflex latency (Granit and Hennatsch, 1956; Homma, et al., 1962). Fusimotor discharges also tend to make the discharge from the primary ending irregular even when the muscle is at a constant length, whereas, after de-efferentation the responses become remarkably regular (Granit, 1957; Matthews, 1964). Under normal conditions many fusimotor fibres become active asynchronously (Matthews, 1964). For these reasons, greater variance of the responses would be expected under conditions where increased fusimotor discharge is assumed. Hence, increased mean response and increased variance in association with decreased

latency are indices of fusimotor tone which do not conflict with established experimental evidence.

The method by which these indices were obtained in the present research was indirect but, nevertheless, not dissimilar from the techniques often used in infra-human research. The measurements were made by observing the extrafusal response by way of EMG, myogram and latency records, and the amount of fusimotor activity was inferred from the three indices used. Similar methods but, of course, at a micro-level are used in animal experiments; in most studies the level of gamma activity is deduced by observing changes in the discharge from spindle afferent fibres isolated as filaments in dorsal roots (Eldred and Fujimori, 1958; Hunt and Paintal, 1958). Any changes which occur in spindle discharge, provided muscle tonus remains unaltered, can be ascribed to changes in fusimotor discharge. This method is used because of the great technical difficulty of recording intrafusal responses directly. However, even direct recording is unreliable because identification of gamma efferent fibres in subdivided ventral root filaments is made by reliance on diameter size and conduction velocity (Matthews, 1964).

The method employed to estimate fusimotor activation of intrafusal fibres in the present research gives indirect but apparently valid information. Although the level of fusimotor activity is inferred from the extrafusal response, the myographic and electromyographic measurements are objective and unequivocal.

For these reasons, there seems to be good evidence that (a) the method is valid and reliable and (b) the indices developed in the present research programme are sensitive enough to warrant continued use.

3. Centrally mediated control of the receptor response

The results of the present experiments have shown that certain types of sensory stimulation such as flashing lights before the eyes, presenting clicks to the ears and contracting remote muscles, have the effect of augmenting the reflex response if applied for short periods but have no effect if used for comparatively long periods. Since these types of sensory input make collateral connections with reticular structures which themselves are known to exert efficient control over the discharge of the muscle spindles, it has been assumed that the augmentation and adaptation found in the present work are the result of regulation of receptor response from regions of the RF (Chapters II, VI, VII and IX).

The particular evidence from the present experiments that the RF can set the muscle spindle sense organ to different levels of sensitivity, confirms the more general view that the RF mediates three neural functions (French, 1960). First, it is implicated in arousal responses; second, it exerts an influence over phasic as well as tonic motor functions; and third, it is capable of modifying

receptor responses. These three functions are apparent in the results of the present experiments.

- (a) Novel stimuli which are presented briefly, alert or arouse the S while continued presentation of the same stimulus apparently results in adaptation of reticular nuclei.
- (b) The augmentation and attenuation of the reflex responses which follow the arousal and adaptation treatments, respectively, indicate the reticular influence on phasic motor response. The direct and indirect descending pathways from supra-spinal regions which are involved in these effects have been discussed elsewhere (Chapter II).
- (c) The predictable changes in the measures of the extrafusar responses, in part, demonstrate modification of the sensory input from the muscle spindle primary endings. For example, there was an obvious decrease in the threshold of the spindles during conditions when supra-spinal facilitation would be expected. For a particular uniform force of tap on the patellar ligament, which was just over the threshold necessary to elicit a brisk reflex, augmented responses were observed during experimental treatments compared with control treatment. In

which lead sessions where the force of the tap
conscious later was reduced during the
1958; Nat experimental treatment until the
experimen responses matched those under control
occurred conditions (Figure 13, Chapter XI and
The Table IIIa, Chapter VII), differences
fatigue. of the order of 300 g were required
mechanism to meet the criterion. This figure
receptor almost certainly represents the combined
adaptation effects of lowered spindle threshold and
of the direct action on the alpha motoneurons
artificial (Chapter IX). However, the combined
(Hall, et effect amounts to about 15 per cent change
adaptation in force on the ligament and even if the
reflex use change in spindle threshold accounted for
a spinal half the effect, it would still be a
1958). marked change.

Thus, the general principles of brain-stem control of the peripheral sense organs by specific pathways are satisfied in the present experiments.

The arousal system involved appears to be a general mechanism which is operated from the RF and is triggered by novel or unexpected stimuli when the S is awake but relaxed. Tactile, auditory, visual and proprioceptive stimuli were found to arouse the Ss so that the mechanism involved was not specific to a particular sense modality. In addition, the process of heightened sensitisation occurs quite involuntarily; the central and peripheral events in the reticular system and in the gamma-spindle system

which lead to the augmented reflex do not reach conscious awareness (Hammond, et al., 1956; Jasper, 1958; Matthews, 1964). The Ss in the present experiments were very surprised by the changes which occurred in the responses.

The adaptation observed was not the result of fatigue. It appears to be an example of a reticular mechanism which filters afferent impulses by dampening receptor sensitivity (Magoun, 1963). The rapid adaptation of reticular nuclei to repeated presentation of the same stimulus has been established with artificial stimuli (Jasper, 1958) and natural stimuli (Bell, et al., 1964) in infra-human animals. Similar adaptation has been found in the human abdominal skin reflex using a non-painful skin stimulus to elicit a spinal withdrawal reaction (Hagbarth and Kugelberg, 1958).

These reticular mechanisms which sensitise and dampen the spindle receptor responses, point to an efficient sub-cortical system for the analysis of primitive forms of sensory stimuli, such as those used in the present experiments.

4. Peripheral modification of receptor response

The results of the pre-strain experiments indicate that a rapid contraction of the rectus femoris muscle under isometric conditions does unload the muscle spindles sufficiently to reduce gamma biasing effects. Only one of the three indices of fusimotor activity could be used because (a) the

muscle tonus changed between control and pre-strain treatments so that no valid comparison could be made between the mean responses of the two sets of trials and (b) the asynchronous MAPs during active contraction of the muscle triggered the timing device so that latency measures were possible only rarely. The assumption that the spindles were unloaded was supported by the significant reduction of the variance during pre-strain trials compared with control trials.

Merton (1953) has suggested that contraction of the intrafusal fibres through gamma efferent discharge would be too slow to prevent the spindle unloading during sudden movements. This is because the fusimotor fibres conduct slowly and if a fast movement is initiated via the direct alpha pathway to the large motoneurons, the contraction of the intrafusal fibres will lag behind the contraction of the main muscle. Also, the tendons are elastic enough to permit some shortening of the muscle (Eldred, et al., 1953; Hunt and Perl, 1960). For these reasons, the spindles would be unloaded and fusimotor activity would have little effect on the sensitivity of the receptor.

The results of these experiments demonstrate that peripheral manipulation of the muscle spindle response is possible to a limited extent in the intact, normal human S by using rapid, active contraction of the muscle.

5. Suggestions for future research

(a) Skin stimulation

A future research programme might investigate the effects of other kinds of skin stimulation and also examine the limits of the skin areas over the responding muscle where facilitation could be found. A map of this kind would show whether facilitation was confined strictly to the area over the responding muscle or whether a larger area was involved.

Further attempts could be made to demonstrate inhibition of the reflex from skin areas over the antagonist muscle because a significant reduction in the reflex response under these conditions occurred rarely in these experiments.

It would be interesting, also, to investigate the effects of contralateral skin stimulation since only ipsilateral stimulation was used in the present experiments.

(b) Visual, auditory and proprioceptive stimulation

An obvious second stage in this research is to examine the temporal relations for the augmentation and adaptation effects of these kinds of stimuli.

The onset of augmentation could be found by tapping the ligament at progressively shorter periods after the onset of the extraneous stimulus. For example, tapping the ligament 1 sec, 0.75 sec, 0.50 sec and 0.25 sec after the initiation of the JM

detected from EMG electrodes over the appropriate muscles.

Conversely, the decay of arousal effects could be found by tapping the ligament at progressively longer periods after the onset of the extraneous stimuli. For example, tapping the ligament after 3, 4, 5, 6 and so on light flashes.

The stimulus parameters necessary to produce an augmented reflex response could be found by systematically altering their intensity. Probably, both individual differences between Ss and between sessions differences within Ss would be encountered.

The effects of bilateral and unilateral stimulation were compared for visual stimulation and a smaller augmentation was observed during monocular stimulation. A similar investigation could be made for auditory and proprioceptive stimulation using both ipsilateral and contralateral sides. No attempt was made in the present experiments to localise the visual stimulus to the contralateral or ipsilateral hemisphere during monocular presentation by confining a ray of light to one side or other of the retina. It might be possible in experiments of this kind to decide whether the arousal and attenuation of reticular and fusimotor activity is bilateral or unilateral in normal human Ss.

(c) The use of Myanesin

Experiments with Myanesin could be conducted to discover whether the drug depressed the augmentation

observed in the present research under normal conditions when three light flashes, three clicks and skin stimulation were used. If a lack of augmentation were found during presentation of these stimuli under Myanesin treatment, it would confirm assumptions made in the present experiments about the supra-spinal influence on the stretch reflex.

(d) Control over rate and amount of muscle extension

The pendulum-hammer used in the present experiments did not permit controlled variation of the rate and amount of muscle extension.

The muscle spindles increase their frequency of discharge as a function of the rate of extension, and the number of endings excited varies as a function of the amount of extension (Chapter II). A plunger mechanism could be designed by taking the geometry of the knee-joint into consideration which would permit these parameters to be varied systematically.

(e) The possibility of detecting sensory discharge emanating from muscle spindles

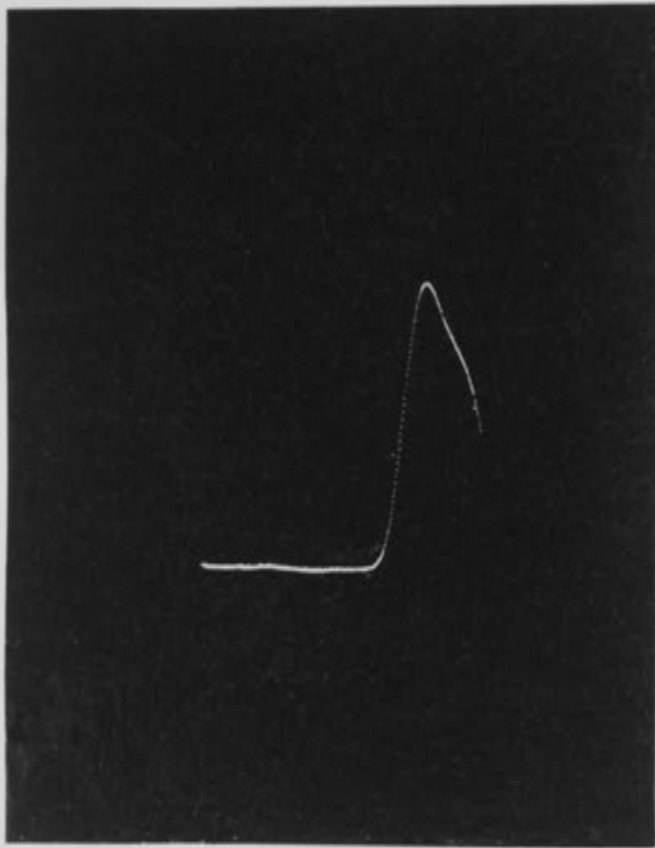
The results of the present experiments have shown that the MAP recorded during isometric reflex contraction of rectus femoris muscle was a discrete, di- or tri-phasic spike without evidence of any observable repetitive activity. Hence, the motor units which participated in the responses apparently fired in a highly synchronous manner. This observation suggests that the discharge of the spindles

also was synchronous otherwise the afferent volley which discharged the alpha motoneurons would have resulted in an asynchronous motor unit response. The sensory action potential would be of minute voltage and embedded in background noise but could be assumed to occur at a fixed point in time after the onset of the mechanical tap on the ligament. Under these circumstances, a computer of average transients could 'extract' the tiny signal after a number of scans (taps on the ligament).

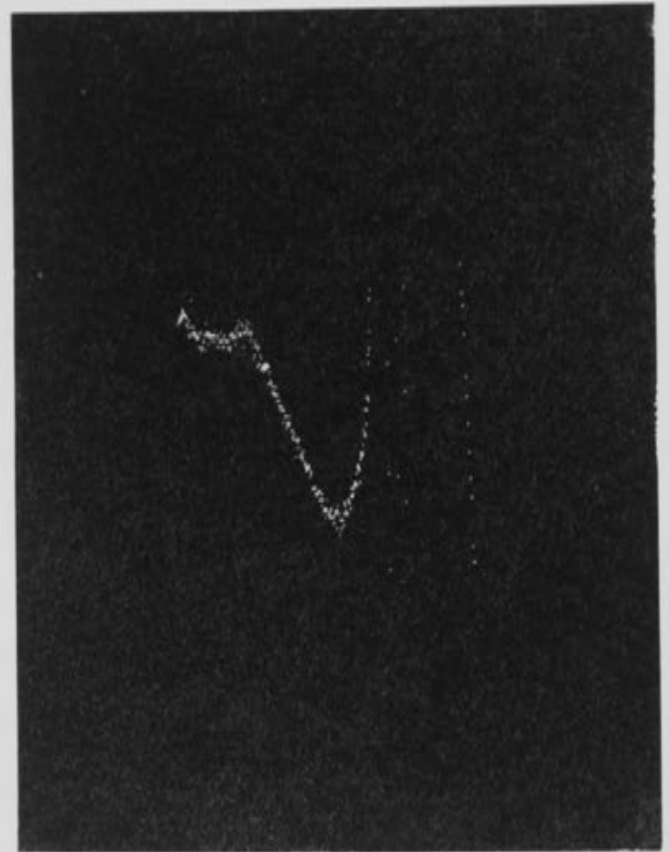
Preliminary investigations with an R.I.D.L. Analyzer (core capacity 400 words) have shown a large, highly synchronous MAP about 20 msec after the onset of the stimulus [Figure 27(a)]. Amplification of the signal showed that a small spike was detected about 1.5 msec after the triggering point after 50 scans [Figure 27(b)]. When the electrodes were moved to a position over the gracilis muscle, the spindles of which were not expected to discharge when the patellar ligament was tapped, a random EMG pattern was observed [Figure 27(c)]. Further, the vibration wave obtained from a magnetic pick-up arm placed on the skin over rectus femoris displayed an entirely different pattern from that found in the three surface EMG records [Figure 27(d)].

Figure 27 (next page)

Examples of the oscilloscope traces observed during different types of experimental conditions from not less than 25 scans of a mechanically elicited, isometrically recorded, patellar reflex with a normal human S. The pulse-height analysis was achieved by the use of an R.I.D.L. (Model 34-27) Analyzer with a 400 word, ferrite core, memory system.



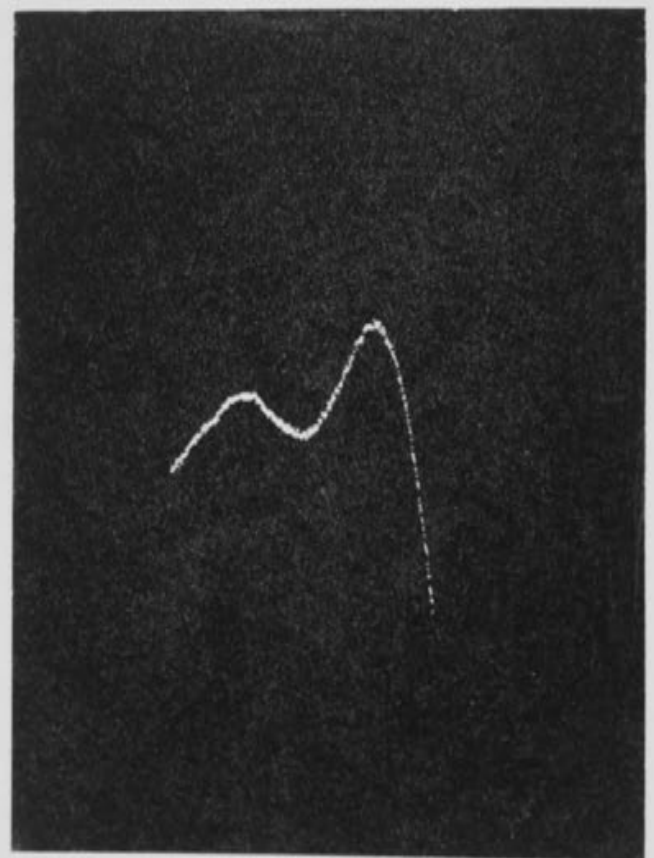
(a) Trace from 100 scans, (400 channels, $75 \mu \text{Sec/channel}$) to show the highly synchronous MAP obtained from surface electrodes over rectus femoris.



(b) Trace from 50 scans (400 channels, $75 \mu \text{Sec/channel}$) to show the small spike about 1.5 msec after the onset of the mechanical stimulus. Electrodes on skin over rectus femoris.



(c) Trace from 50 scans (400 channels, $75 \mu \text{Sec/channel}$) to show the random pattern obtained when the electrodes were moved to the skin over gracilis.



(d) Trace from 25 scans (400 channels, $75 \mu \text{Sec/channel}$) to show the vibration wave obtained from a magnetic type pick-up arm over rectus femoris.

These results, which were similar for the five Ss used, support the view that the sensory discharge can be detected from surface electrodes under conditions where the Ss are highly trained in relaxation and where control is exercised over environmental stimuli. However, the results are inconclusive because the possibility remains that the mechanically induced vibration of the muscle produced the spike as an artifact. Unless the signal can be shown to obey a biological law, such as refractoriness, its origin will remain uncertain.

Tests of refractoriness could be made in two ways. First, two mechanical taps could be given on the patellar ligament very close together in time to see whether the small spike behaved in the refractory manner expected of an action potential (Matthews, 1966). Second, a test could be made by electrically stimulating the afferent nerve to fire the spindles anti-dromically and then applying a mechanical tap to the ligament in the refractory period (Lance, 1966). A recovery curve could be plotted by progressively lengthening the time interval between electrical and mechanical stimulation. In this case, it would be better to use gastrocnemius with the S lying prone so that the popliteal nerve and achilles tendon would be accessible to electrical and mechanical stimulation, respectively. The gastrocnemius muscle also ought to give 'a much better action potential than will the numerous small nerve branches running through the quadriceps' (Matthews, 1966).

Should the technique prove to be successful, it would provide a more direct method of assessing fusimotor activity; the receptor responses could be monitored rather than the extrafusal responses and the observations would be uncontaminated by the supraspinal influences which impinge directly on the alpha motoneurons. Under these conditions, heightened fusimotor activity would be expected to result in an increased spindle discharge so that the recorded "sensory spike would become larger in amplitude (voltage) compared with control trials. Further, the biasing of the spindle would be expected to decrease the latency of the sensory spike compared with control spikes. Both of these effects might be observed with electronic averaging computers now available.

6. Some speculations about spindle behaviour

Some of the treatments used in the present experiments indicate that the augmentation of the reflex response results, in part at least, from an increase in the sensitivity of the spindle primary ending by fusimotor biasing.

This form of influence on the receptor is indirect, that is, phasic stretch reflexes such as the patellar reflex 'run through the alpha system without direct gamma control' (Granit, 1957). Under these circumstances, the lowered threshold of the spindle observed in the experiments must have occurred prior to the tap on the ligament and while the muscle remained at a fairly constant resting length.

Matthews (1962) and Brown, et al. (1965) have classified two functionally distinct types of fusimotor fibre (static and dynamic) on the basis of the response of the spindle primary ending to stimulation of different single gamma fibres. Stimulation of both types of fibre increased the discharge of the primary ending when the muscle was at a constant length. Some recent specific evidence permits speculation about the involvement of the static gamma fibre (which powerfully excites the primary ending when the muscle length is constant) in the biasing process in the present experiments.

First, Alnaes, et al. (1965) have reported that activity in the static fusimotor system appears to depend entirely on facilitatory influences descending from the brain. Second, Boyd (1966) has shown that stimulation of appropriate gamma fibres while the spindle was at a constant length, resulted in local contraction of both the nuclear bag and nuclear chain fibres (in some spindles the contraction was great enough to cause visible extension of the equatorial region of the intrafusal fibres which is the portion where the afferent endings ramify). Boyd concluded that 'it seems probable that all the gamma fibres involved are static'.

For these reasons, it seems that the static fibres of the fusimotor system probably were the principal biasing influence in the present experiments.

7. General conclusion

The present series of experiments have demonstrated that control is possible over environmental and organismic variables which affect the stretch reflex so that very consistent responses are achieved for a uniform stimulus.

The subsequent systematic manipulation of these kinds of variables has shown a relationship between assumed activation of reticular neurones and a spinal reflex by way of direct and indirect descending pathways. These centrifugal influences have been shown to affect the reflex by direct action on alpha motoneurones and indirectly by fusimotor sensitisation of muscle spindles. Both pathways seem to operate together during arousal to heighten the sensitivity of the alpha motoneurones and to alter the functional reactivity of the spindles.

Thus a reciprocal relationship is possible between central and peripheral events in the gamma-spindle system. On the one hand, the muscle spindles provide the CNS with information about the state of the muscles whilst, on the other hand, the gamma activity grades the efficiency of the response (across parameters of force and time, such as force of contraction and latency of response following stimulation) according to the needs of the organism. Both kinds of impulses play a part in subconscious nervous control of muscular response, the spindles send Ia afferent impulses which initiate the stretch reflex

contraction and the gamma efferents transmit impulses which set the threshold of the receptor.

More generally, afferent fibres from muscles and other types of receptors make collateral connections with the brain-stem RF which apparently acts 'as an important collecting net for influences destined to mobilise the gamma system' (Granit, 1957). Such a system seems to be well suited to setting the excitability level of the spinal cord so that it is compatible with the general arousal level of the S. For example, when stimuli alert the S, the muscles are prepared by fusimotor sensitisation to perform a highly efficient movement (that is, one with a large contractile force, and a short latency of response). This would be a suitable preparation for evasive or protective action should the S consciously decide upon such action. At the other extreme, under quiet conditions the S may fall asleep, in which case the muscles relax and only minimal responses occur.

The general results of the present programme of research indicate that under conditions of careful control, the measures of the phasic stretch reflex accurately reflect the level of fusimotor discharge which, in turn, is related to supra-spinal activity. This conclusion is consistent with the view of Granit (1957) that

the gamma-spindle system is probably the most sensitive indicator we possess of what in present-day brain physiology is called

'activation' and is assumed to arise in the brain stem (Magoun's reticular activating system). It has the advantage over the EEG that one knows what one measures and knows when the effect is excitation and when inhibition.

APPENDIX A

FIGURES 28 TO 36

Details of the head of the pendulum-beam and circuit diagrams for the electrical apparatus constructed for the experiments.



APPENDIX A

FIGURES 28 TO 36

Details of the head of the pendulum-hammer and circuit diagrams for the electrical apparatus constructed for the experiments.

APPENDIX FOR MEASURING FORCE
BY MEANS OF CONTRACTION



AMPLIFIER FOR MEASURING FORCE OF ISOMETRIC CONTRACTION.

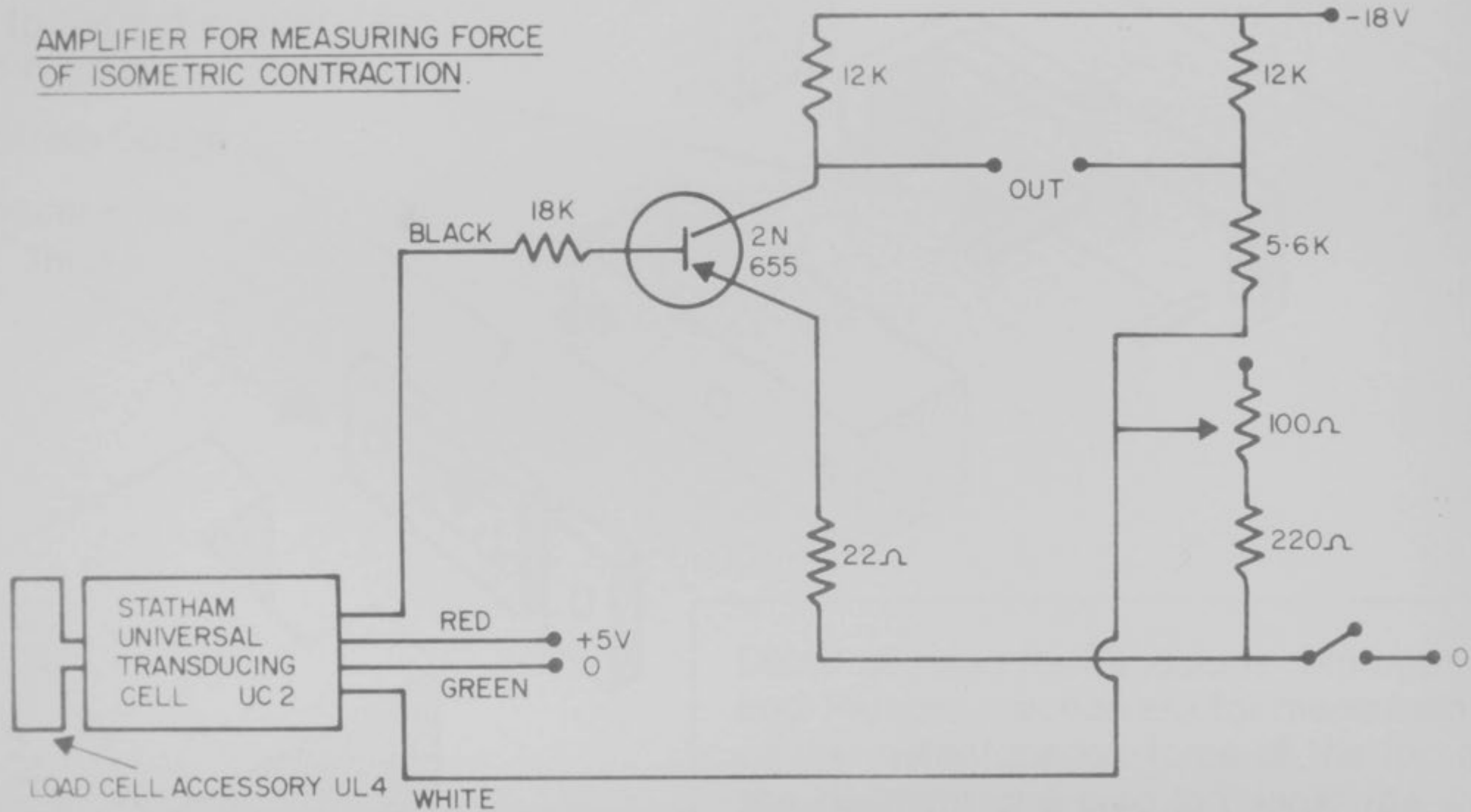


FIGURE 28

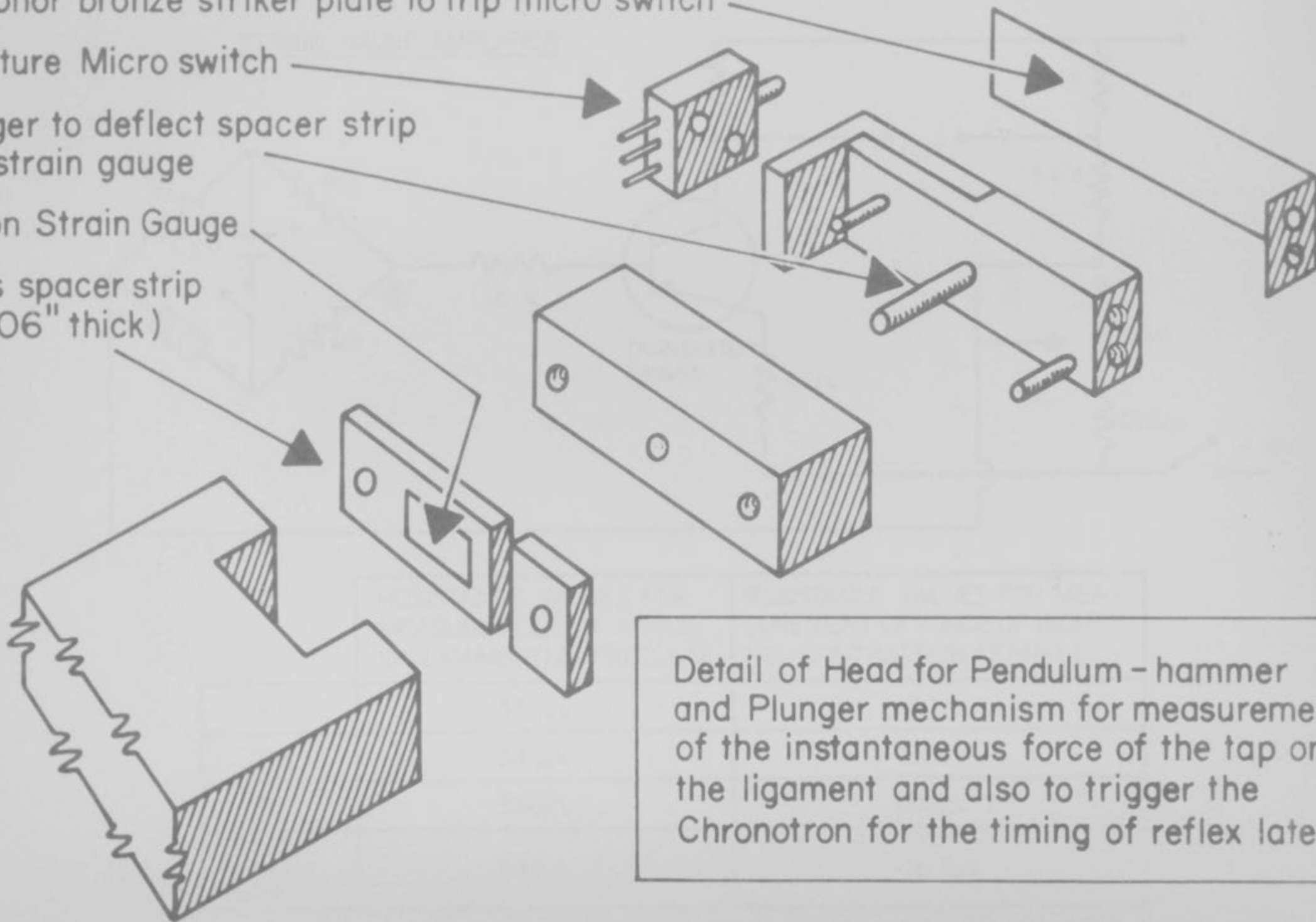
Phosphor bronze striker plate to trip micro switch

Miniature Micro switch

Plunger to deflect spacer strip
and strain gauge

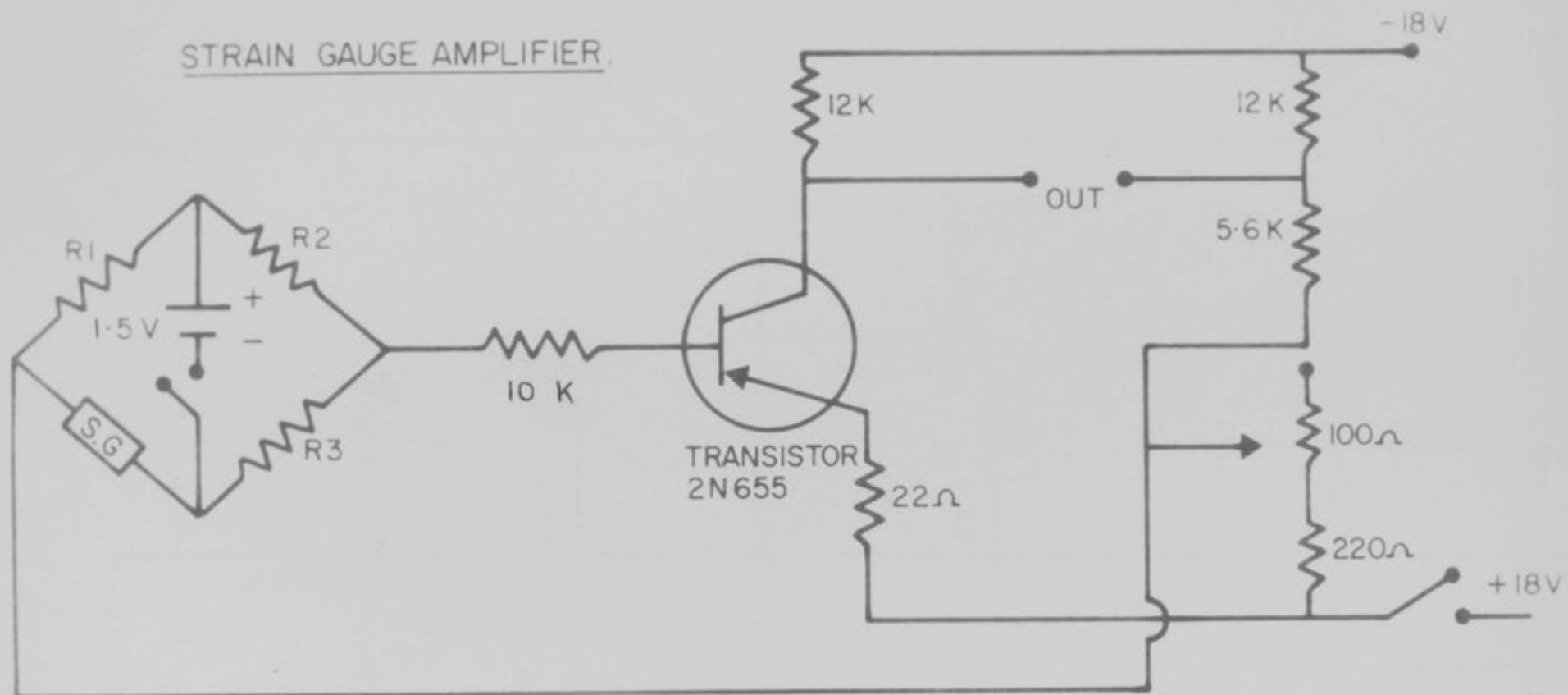
Silicon Strain Gauge

Brass spacer strip
(.006" thick)



Detail of Head for Pendulum - hammer
and Plunger mechanism for measurement
of the instantaneous force of the tap on
the ligament and also to trigger the
Chronotron for the timing of reflex latency.

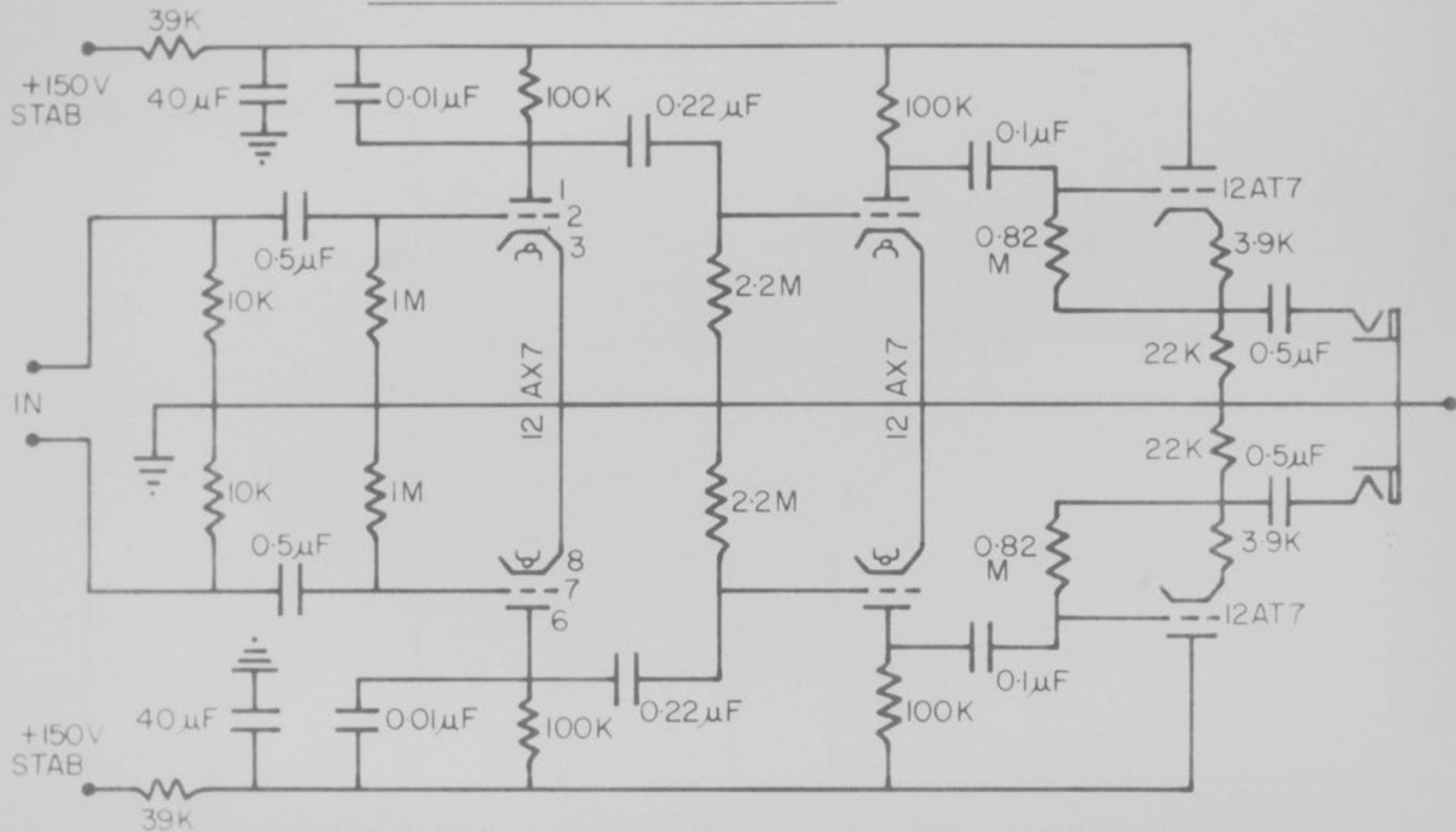
FIGURE 29



| | RESISTANCE VALUES FOR MEASUREMENT OF FORCE ON LIGAMENTUM PATELLAE. | RESISTANCE VALUES FOR MEASUREMENT OF FORCE OF ISOMETRIC CONTRACTION AT ANKLE. |
|---------------------|--|---|
| R1 | 345 Ω | 120 Ω |
| R2 | 345 Ω | 120 Ω |
| R3 | 350 Ω | 120 Ω |
| P TYPE STRAIN GAUGE | 346 Ω | 116.6 Ω |

FIGURE 30

PUSH-PULL AMPLIFIER FOR EMG.

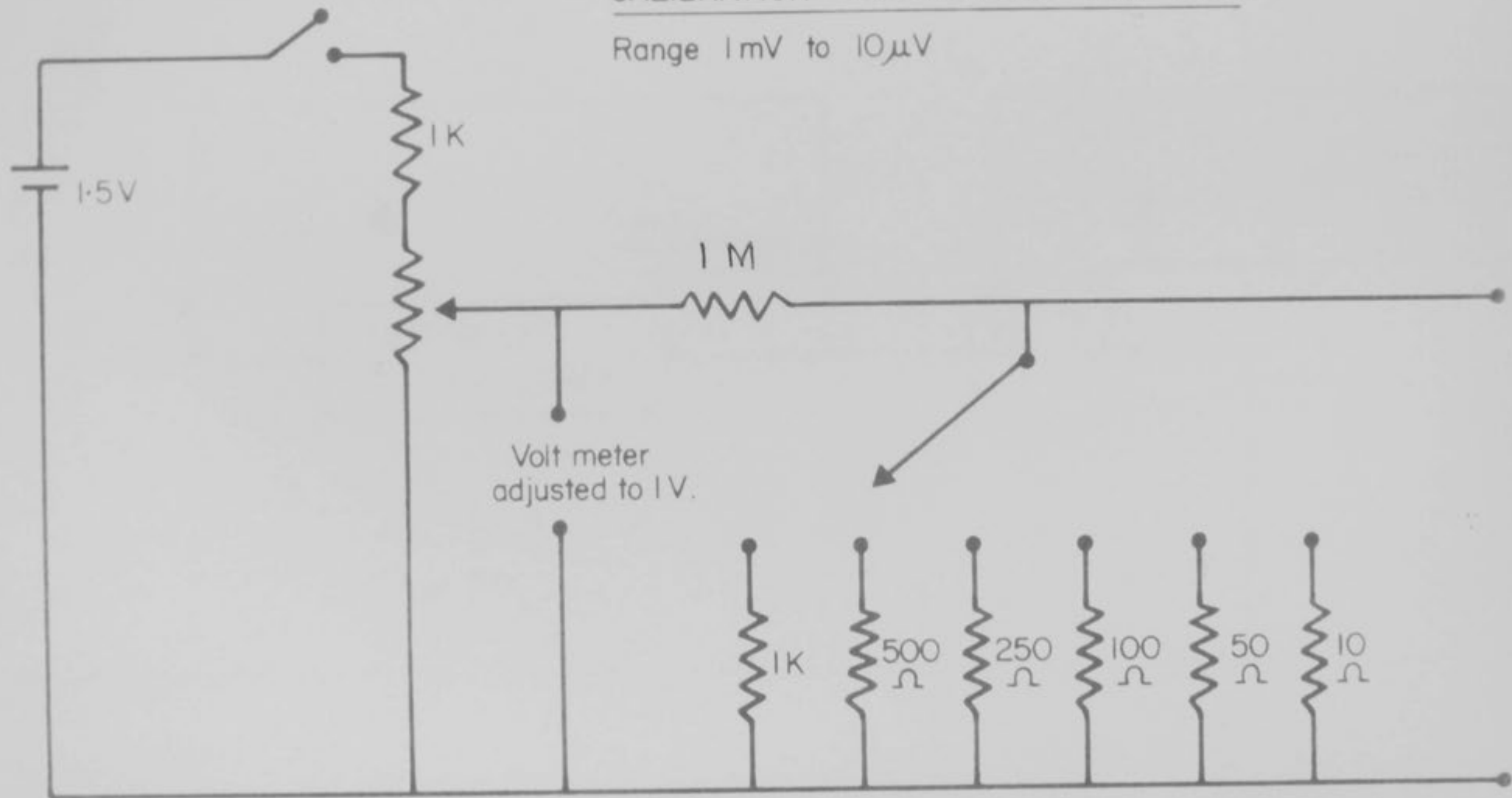


Gain \approx 2.5K 50% at 1.5 cps 80% at 3 cps 90% at 4 cps
 Hum out \approx 60 mV peak to peak. Equiv. 0.01 mV input.

FIGURE 31

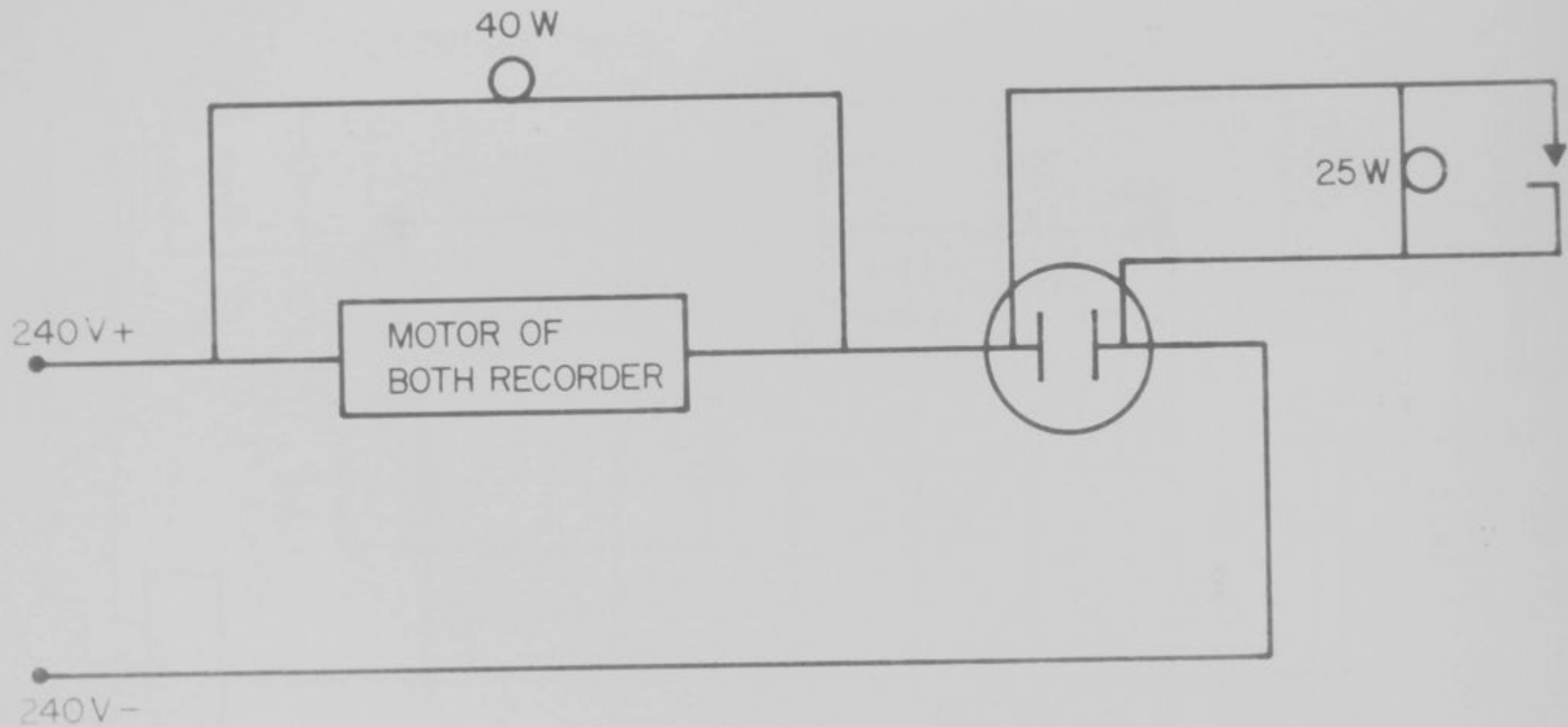
CALIBRATION INSTRUMENT FOR EMG.

Range 1 mV to 10 μ V



Resistors : 1% accuracy , high stability.

FIGURE 32



Method of preventing electrical interference to EMG when switching on pen recorder motor for paper travel.

FIGURE 33

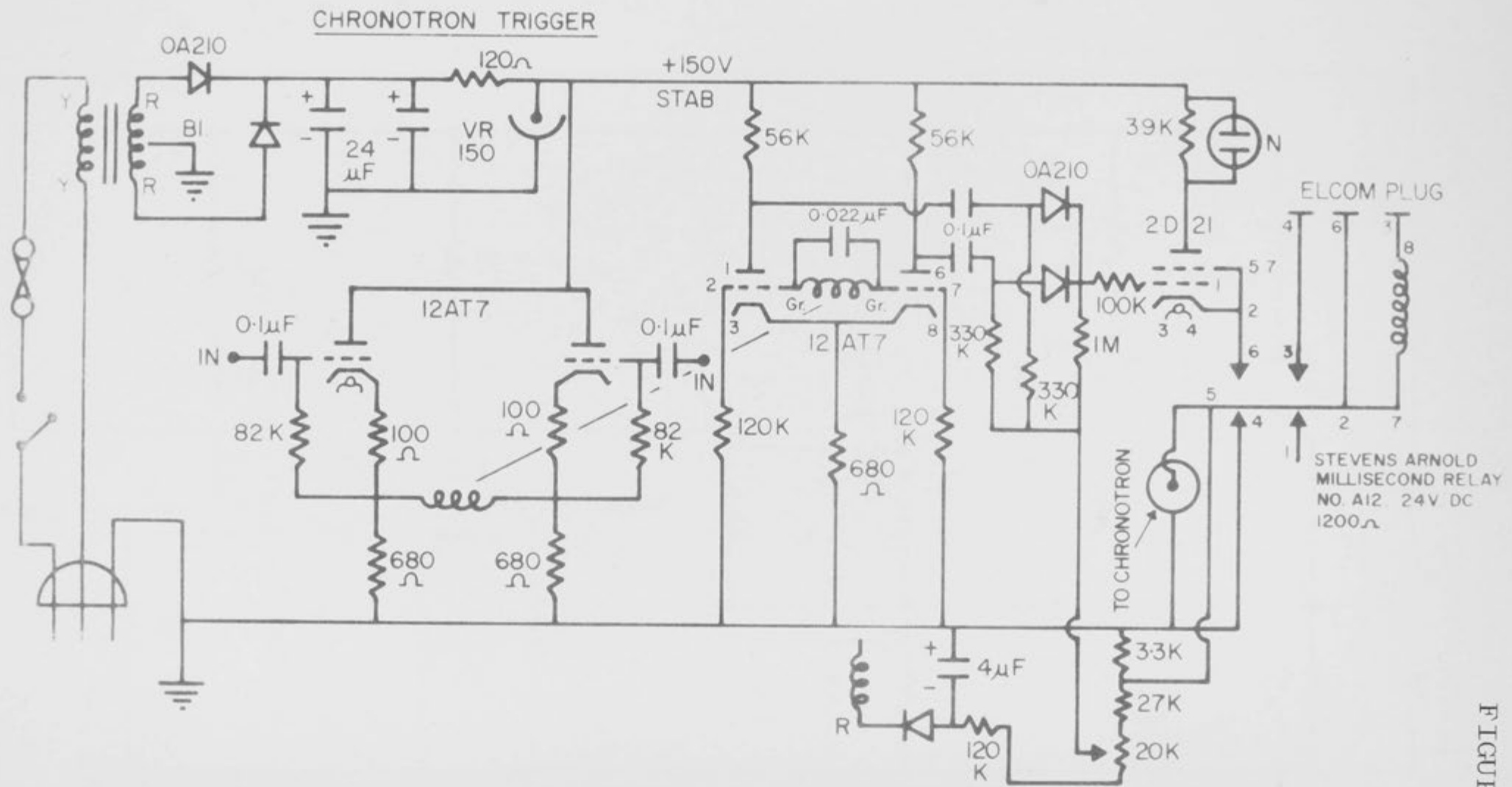


FIGURE 34

VISUAL INDICATOR CIRCUIT TO MONITOR EMG SIGNALS.

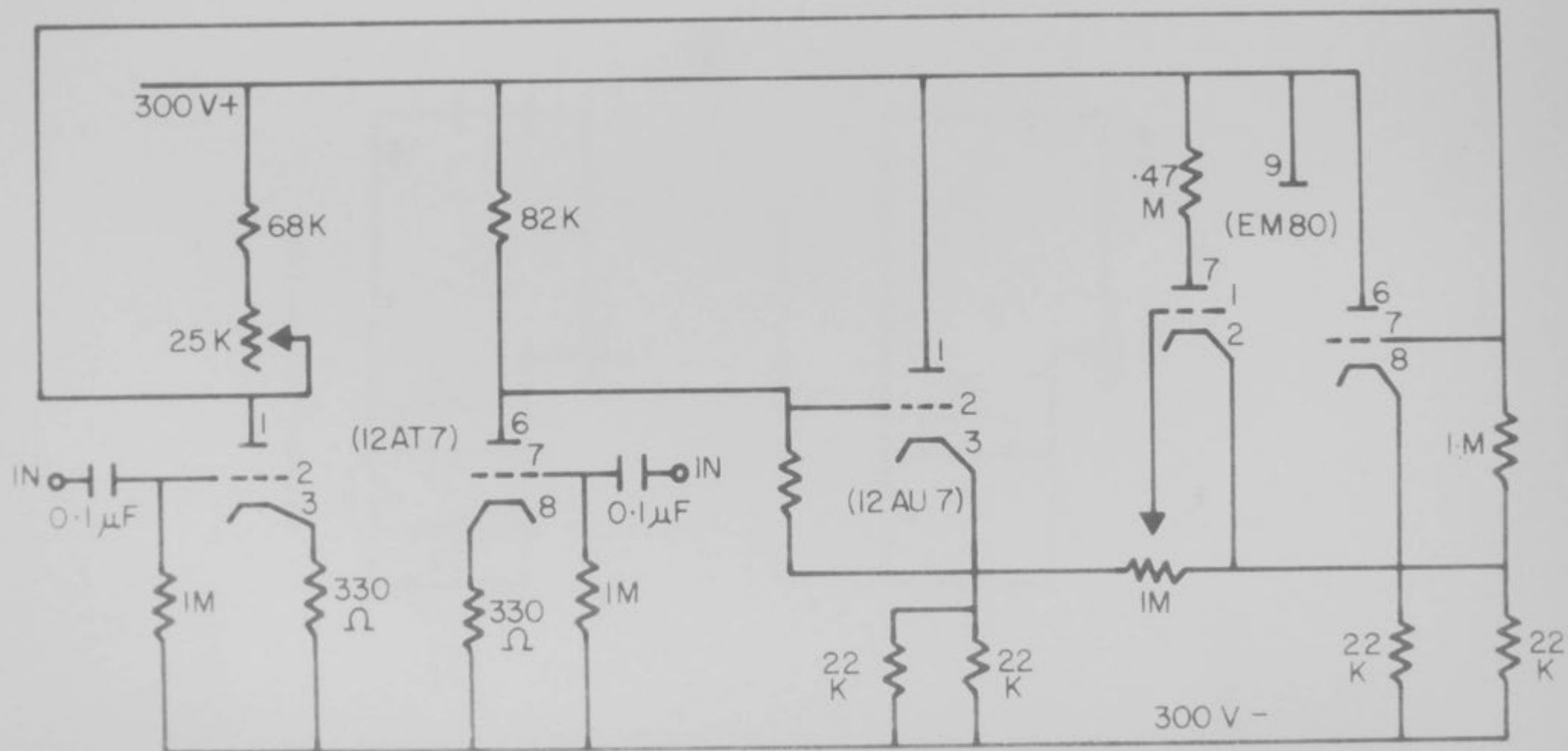
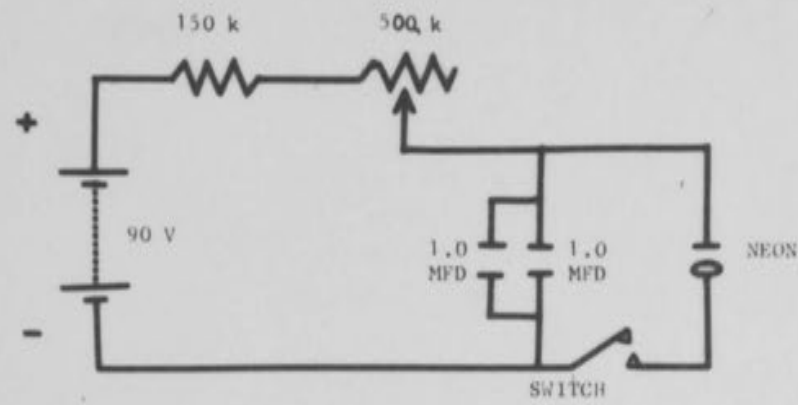
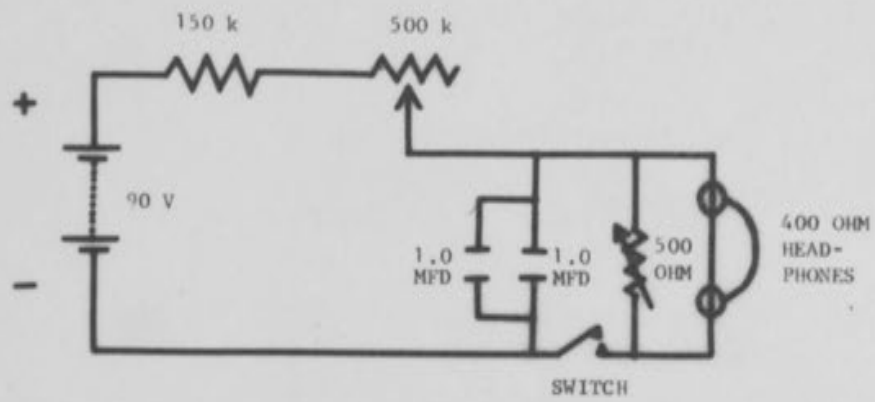


FIGURE 35

FIGURE 36



CIRCUIT FOR FLASHING LIGHT



CIRCUIT FOR CLICKS TO HEADPHONES

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