#### ABSTRACT

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D. Watt, "Modes of Control in Some Antigravity Muscles in Man", Department of Physiology, M.Sc. thesis.

When an individual lands from a step to the ground, his antigravity muscles must oppose and terminate his downwards movement. It is often assumed that lengthening of involved postural muscles generates functional stretch reflexes that automatically match the strength of contraction of these muscles with the loads imposed. This contention was examined in the gastrocnemius and soleus muscles.

The latency of the functional stretch reflex, as described by Hammond, Merton, and Sutton (1956) in the arm, was first determined in the gastrocnemius – soleus muscles. Electromyographic activity in these muscles, and the forces exerted by the foot, were then examined during steps to the ground, repetitive hops, and sudden, unexpected falls.

The functional stretch reflex was found to have a latency of 119.5 msec. (S. E. 3.5 msec.). When landing from a 15-inch step to the ground, gastrocnemius - soleus e.m.g. activity started 152 msec. (S. E. 14.9) before, and ended 131 msec. (S. E. 15.5) after, the instant of contact with the ground. When hopping, the duration of e.m.g. activity after landing was more prolonged (262.7 msec., S. E. 10). After initiating an unexpected fall, there was a very constant e.m.g. latency of 75 msec. (S. E. 1.4 msec.).

It is concluded that the precisely controlled activity in the antigravity muscles of the lower limb during landing from a step to the ground originates in the form of a pre-programmed unit released centrally well before the moment of impact. A stretch reflex may function, however, in initiating the upwards motion in repeti-

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It is concluded that the precisely controlled activity in the antigravity muscles of the lower limb during landing from a step to the ground originates in the form of a pre-programmed unit released centrally well before the moment of impact. A stretch reflex may function, however, in initiating the upwards motion in repetitive hopping. A reflex contraction to sudden weightlessness may also play a role in hopping and running. Modes of Control in Some Antigravity Muscles in Man

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D. Watt

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Modes of Control in Some Antigravity Muscles in Man

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by

D. Watt, B.Sc.

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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1969

1969

#### ACKNOWLEDGEMENTS

Many individuals have assisted me in carrying out this research programme, and in the preparation of the following thesis. Certainly, those who worked the hardest, in the physical sense, were my subjects, without whose patience, exertion, and functioning gastrocnemius muscles, this programme would not have been possible.

A special word of thanks is gratefully given to Werner Ferch and the personnel of the McGill Electronics Workshop for their invaluable advice and practical assistance in evolving and constructing the electronic systems used.

I am also indebted to the Departments of Mechanical Engineering, and BioMedical Engineering, of McGill University, for the loan of various equipment used.

Thanks to Dr. John Outerbridge, and to Dugald Taylor, for their explorations of statistical methods.

I am very grateful as well to Jo Ann Brown, of the BioMedical Engineering Unit, for her patience and effort in typing this manuscript.

Particularly, however, I would like to thank Dr. G. Melvill Jones, my research director, for his many suggestions, frequent guidance, and direct participation in all aspects of the project. Ultimately, a research programme of this sort must direct the neophyte into an approach and philosophy of scientific investigation, rather than merely being a mechanical examination of one specific hypothesis. I am exceedingly grateful to Dr. Melvill Jones for Having imparted to me some of his overall concept of science and the scientific method; the limiting factor has been my ability to learn, not the teaching I have received.

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# TABLE OF CONTENTS

I.	Introduction	1
Н.	Literature Survey	
	1. Introduction	2
	2. Movements as Reflex Responses	2
	3. The Cerebral Cortex	3
	4. Descending Pathways	7
	5. The Motoneurone	10
	6. The Neuromuscular Junction	12
	7. Skeletal Muscle	13
-	8. The Muscle Spindle	21
	9. The 🗴 Loop	30
	10. Higher Control of the $oldsymbol{\delta}$ Loop	39
	11. The Long-Loop Reflex	42
	12. Review Articles	43
Ш.	Statement of Problem	
	Part 1	44
	Part 2	44
	Part 3	46
	Part 4	46
	Part 5	46
IV.	Methods	
	General	48
	Part 1	50
	Part 2	54
	Part 3	62
	Part 4	64
	Part 5	67

Page

.

٧.	Results	Page
	Part 1	70
	Part 2	73
	Part 3	90
	Part 4	98
	Part 5	103
VI.	Discussion	107
VII.	Summary	124
Append	dices	126
Referer	nces	129

.

# LIST OF FIGURES

Figure	Subject	Page
1	Cortical representation of movement	6
2	Motor areas of the cerebral cortex	6
3	Descending tracts in the thoracic spinal cord	11
4	Motor nuclei of the ventral horn in the cord	11
5	Microstructure of a muscle fibre	16
6	Ultrastructure of a myofibril – long.section	16
7	Ultrastructure of a myofibril – cross section	18
8	Afferent/efferent supply of muscle , muscle spindle	26
9	Muscle spindle and its innervation	29
10	Apparatus for recording functional stretch reflex	51
11	Load transducing platform	55
12	Composite recording arrangement	57
13	Computer averaging of e.m.g. response	59
14	Electromagnetic dropping device	65
15	Composite oscillation apparatus	68
16	Monosynaptic e.m.g. response to tendon tap	71
17	Voluntary e.m.g. response to an auditory cue	71
18	E.m.g. response to an applied and maintained force	71
19	E.m.g. response to landing from a step to the ground	74
20	E.m.g. response to a step-superimposed tracings	75
21	Computer-averaged response to 150 steps	77
22	Graph: $C \rightarrow e.m.g.end$ versus height of step	79
23	Graph: C $\rightarrow$ e.m.g. end versus height of step	80
24	Graph: C-+e.m.g. end versus height of step	81
25	Graph: C→max. F. versus height of step	85
26	Graph: $C \rightarrow max dF/dt$ versus height of step	85
27	Graph: e.m.g. start $\rightarrow$ C versus height of step	86
28	Graph: max.dF/dt versus height of step	86



29	Graph: e.m.g. start -> C versus height of step	87
30	Graph: C- max.e.m.g. activity versus height of step	87
31	Measurement of ankle angle during a step	88
32	Gastrocnemius e.m.g. response to repetitive hopping	91
33	E.m.g. response to a hop – superimposed tracings	91
34	Computer – averaged response to 200 hops	94
35	Graph: C- max. F. versus rate of hopping	95
36	Graph: C→max.dF/dt versus rate of hopping	95
37	Graph: Max. F. versus rate of hopping	96
38	Graph: max.dF/dt versus rate of hopping	96
39	Graph: e.m.g. start — C versus rate of hopping	97
40	Graph: C-e.m.g. end versus rate of hopping	97
41	The effect of height on landing from a fall	99
42	Graph: start of fall→e.m.g. start versus height of fall	100
43	Graph: summary of results of experiments: involving falls	102
44	The effect of vertical oscillation on the gastrocnemius e.m.g.	104
45	Graph: e.m.g. spike frequency versus position in cycle	105
46	Graph: summary of results of experiments involving oscillation	106
47	E.m.g. response to landing from a step	109
48	Force buildup in human gastrocnemius muscle	109
49	H–reflex excitability after conditioning afferent volley	113
50	E.m.g. response to landing from a hop	113
51	Time from leaving ground to the e.m.g. start in a hop	122

.



# LIST OF TABLES

.

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Table	Subject	Page
1	Mechanical properties : slow and fast muscle	18
2	Classification of muscle spindle afferents	26
3	Summary of results – Part I	72
4	Statistical comparison of points on graph, Figure 24	82
5	Summary of stepping results, Group I subjects – R.P.	84
6	Soleus e.m.g. response to a 15-inch step	88
7	Summary of results – ankle angle during a step	89
8	Natural hopping frequency, 8 subjects	89
9	Summary of hopping results, Group I subjects	93
10	Soleus e.m.g. response to a hop at preferred frequency	94

#### INTRODUCTION

Man may be considered a machine that moves and a large part of his body is adapted specifically for providing motion. His muscles are the motors, his skeleton is the framework, and his central nervous system and its peripheral connections are the controlling system.

A vast range of movements are required, from the cumbersome charge of a football lineman to the intricate manipulations of a fine craftsman. Yet these extremes are not far removed except by scale, for the lineman must still control with precision both the time and strength of every muscle action in his explosion of motion. And both must coordinate many individual muscles to correctly perform the desired act.

The system that integrates these actions is complex in both structure and function, yet it is highly reliable and capable of adapting to new situations as they arise. It operates continuously, predominantly below the level of conscious thought, and correctly produces the appropriate motor act guided by a variety of external and internal stimuli.

It is the aim of this study to examine a small part of the way in which man controls his muscles, particularly those of the lower leg, involved in opposing the forces generated by landing from stepping, hopping, and falling movements.

#### (1) Introduction

It is necessary first to broadly survey the general field of muscle control. One is immediately struck by the wealth of material available, and by the fact that there are many controversial areas in which unanimous agreement has not yet been reached. Knowledge of structure and function have evolved hand in hand and cannot be divorced from each other completely. Yet, for purposed of clarity, it is possible at this point to give a fairly complete account of each as a separate entity. Emphasis will be laid upon the so-called "& - loop" system as it is perhaps most intimately involved in this project.

#### (2) Movements as Reflex Responses

Sherrington saw body movements as being the reflex response to a number of parallel external and internal stimuli. The brain is the great integrator of all the inputs and it selects the appropriate output. This goes to the final common pathway of the motoneurone and a muscular response results. He visualized the cerebellum as being a centre for changing movements. That is to say, the cerebrum is the area in which an appropriate motor act (e.g., a coordinated limb movement, not the contraction of one specific muscle) is conceived and commanded. Constant movements, on the other hand, such as moving a hand away from the body at a steady rate, or running, are mediated by the more automatic cerebellum, which cannot initiate a purposeful voluntary movement by itself. (Sherrington, 1906).

It is important to realize that it is actually the motion of his body and limbs relative to his environment that man directs in moving, rather than individual motor units or muscles, a point suggested by Sherrington, as well as by Horsley (1909) and Walshe (1943).

# (3) <u>The Cerebral Cortex</u>

(a) Introduction

It has been known for many years that specific areas of the cerebral cortex exist that control movement. The motor cortex was mapped in animals as early as 1876. (Ferrier, 1876). Evidence that a similar situation existed in man was later in coming, but the work of Perfield and many others has now provided us with a detailed description of the areas of the brain that function in controlling voluntary movements.

#### (b) Histological Structure

The cerebral cortex is composed of six fundamental layers. (Brodmann, 1909). These are, from the external surface inwards: 1. the molecular layer, 2. the external granular layer, 3. the external pyramidal layer, 4. the internal granular layer, 5. the internal pyramidal layer, and 6. the multiform layer. The molecular layer contains relatively few cells; some have horizontal axons and some are Golgi type II cells. It also contains dendrites and axons from deeper layers, forming a fairly dense mass of fibres. The external granular layer is distinguished by the presence of many small triangular cells. The external pyramidal layer is composed primarily of neurons of pyramidal shape.

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Their axons enter the white matter, chiefly as association or commissural fibres. The internal granular layer contains a great number of small, stellate, cells. The internal pyramidal layer consists mainly of medium and large-sized pyramidal neurons. Their axons enter the white matter chiefly as projection fibres and to a lesser extent as association fibres. The multiform layer contains largely spindleshaped cells whose long axes are perpendicular to the cortical surface. (Truex and Carpenter, 1964).

# (c) Cytoarchitectural Mapping

The cortex does not have the same structure everywhere, with variations in overall thickness, relative thickness and density of its layers, and the arrangement and amount of cells and fibres in different areas. These differences may be used to produce a cytoarchitectural map of the cortex. Several authors have done this (Campbell, 1905, Brodmann, 1909, von Economo, 1929, Vogt and Vogt, 1919, Beck, 1929, Rose, 1935); the main problem being one of deciding how fine a distinction is required to define an area, as the number of areas depends on this. Brodmann's classification into 47 areas is probably the most accepted. The significance of this classification lies in the fact that many functional areas of the cortex correspond exactly to areas defined by him.

# (d) Physiological Mapping - Areas of Motor Function

Area 4 is the primary motor area, and is located on the anterior wall of the central sulcus and adjacent portions of the precentral gyrus. It contains the giant pyramidal cells of Betz, the axons of which constitute the large corticospinal tract fibres. (Holmes and May, 1909, Levin and Bradford, 1938). Many other fibres also arise from smaller cells in the area and go down the same tract. It is a pathway intimately concerned with the generation of highly skilled voluntary movements.

Electrical stimulation of this area of the brain usually results in specific movements involving functional muscle groups rather than a single muscle, although contractions of one muscle only have been observed. Charts of the human cortical representation of movement in area 4 have been developed by several investigators (Foerster, 1936a, 1936b, Penfield and Boldrey, 1937, Scarff, 1940, Penfield and Rasmussen, 1950, Penfield and Jasper, 1954), and these all show similar somatotopic localization. This is diagrammed in Figure 1.

Brodmann's area 6 lies immediately in front of the primary motor cortex. It runs dorsoventrally along the whole lateral aspect of the frontal lobe and is continued on the medial surface to the sulcus cinguli. (Truex and Carpenter, 1964). It has been subdivided into areas a and b by Foerster (1936b). Area a is further divided into a and  $\beta$  parts. Electrical stimulation of area 6a a produces responses similar to those of area 4, but stronger stimuli are required. Area 6a  $\beta$  produces more general movements, such as rotation of head, eyes, and trunk to the opposite side. Stimulation of area 6b produces rhythmic coordinated movements, especially of the face. (Truex and Carpenter, 1964).

Another area of the brain will also produce movements upon electrical stimulation. This has been designated the supplementary motor area (Penfield and Rasmussen, 1950), and occupies the medial surface of the 5



# Fig. I.

Diagram of the left cerebral hemisphere of man. The somatotopic representation of movement in the primary motor area is indicated.



# Fig. 2.

Diagram of the left cerebral hemisphere of man. The various areas concerned with motor function as determined by physiological mapping are indicated.

superior frontal gyrus rostral to area 4. It also shows complete somatotopic representation of movement. (Woolsey et al., 1951).

A secondary motor area has been described in the monkey; it lies along the superior bank of the lateral sulcus and extends posteriorly into the parietal lobe. (Woolsey, 1958). It is not yet sure whether it may be termed a secondary motor area in man, though stimulation of this area may produce a desire to make a specific movement. (Penfield and Rasmussen, 1950).

There is one other small area that lies just in front of the premotor cortex that is particularly concerned with voluntary eye movements. It constitutes part of Brodmann's area 8, and is termed the frontal eye field area. (Foerster, 1931, Penfield and Rasmussen, 1950).

The areas described above, then, make up the cerebral cortical representation of movement. They no doubt are of primary importance in initiating a voluntary muscular response. Figure 2 summarizes their locations.

# (4) Descending Pathways

Corticofugal fibres originating in the areas described above are projected widely to the spinal cord, the brain stem, and subcortical telencephalic nuclei.

Many fibres originating in the primary motor cortex travel down the cord in the corticospinal tracts. Roughly eighty per cent of these cross over at the level of the medulla in the pyramidal decussation and constitute the lateral corticospinal tract. The remaining twenty per cent travel down the cord as the anterior corticospinal tract and either cross over at the level of their innervation, or remain on the ipsilateral side. The anterior corticospinal tract extends only down as far as the upper thoracic cord. A large number of fibres from the primary motor cortex do not use the corticospinal tracts, however; they remain extrapyramidal.

While some fibres from the premotor cortex appear to use the corticospinal pathways, the vast majority are extrapyramidal. They travel to the putamen, globus pallidus, thalamus, hypothalamus, red nucleus, and reticular formation. (Truex and Carpenter, 1964).

Fibres from the supplementary motor area run down the corticospinal tracts bilaterally (Bertrand, 1956); their function is unsure. The course of fibres from the secondary motor area is not known. Lastly, the frontal eye fields area sends its axons out via the corticoreticular or corticotectal paths.

The corticospinal tracts are important, but not essential, routes for impulses that result in volitional movements. They are especially important in isolated individual movements of the fingers and hand which are the basis of skilled, fine, control. Evarts (1968) has shown that high conduction velocity pyramidal tract neurones tend to be active during periods of movement, that this activity just precedes the peripheral e.m.g. activity, and that the amount of pyramidal tract neurone activity is proportional to the force exerted by the moving part. However, section of the pyramidal tract does not abolish movement, or in some circumstances even alter it greatly, as much of it is mediated by cortically originating extrapyramidal fibres (COEPS). (Ruch and Patton, 1966). Many of these fibres originate from the primary motor area, and the vast majority of efferents from other motor areas are COEPS.

There are descending pathways other than the pyramidal tract and COEP fibres concerned with voluntary muscle control in its broader sense. The reticulospinal tracts provide a system of fine fibres descending in the anterior and anterolateral portions of the spinal cord, coming from the pontine and medullary reticular formation. The brain stem reticular formation can facilitate or inhibit voluntary movement and reflex activity, as well as influence muscle tone. It does this by acting upon motoneurones, which innervate the intrafusal muscle fibres in muscle spindles (to be described). Inhibition of the muscle spindle comes from the medullary reticular formation, while facilitation comes from more rostral regions. The downgoing impulses travel in the reticulospinal tracts.

The vestibulospinal tract originates in the lateral vestibular nucleus of the medulla, which receives fibres from the eighth cranial nerve and cerebellum, and travels downwards on the same side near the anterior periphery of the cord. The vestibular nuclei exert a facilitatory influence upon the reflex activity of the spinal cord and the system that sets muscle tone. The lateral vestibular nucleus receives somatotopically organized fibres from the cerebellum, and it is likely that cerebellar as well as vestibular influences upon muscle tone and posture also travel via the vestibulospinal tract.

The rubrospinal tract is a small bundle of fibres travelling anterior to and partly mixed with the lateral corticospinal tract down to the

9

lower thoracic segments. It originates from the red nucleus, and probably exerts a facilitatory influence upon flexor muscle tone. (Pompeiano and Brodal, 1957).

The descending pathways mentioned (as they would appear in the upper thoracic region) are shown in Figure 3.

#### (5) The Motoneurone

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#### (a) 🗙 Motoneurones

The efferent fibres running down the cord must eventually synapse with a motoneurone. This may be a direct connection, or via an interneurone, and it occurs at the correct spinal level to innervate a particular muscle. Motoneurones are located in the anterior horn of grey matter throughout the length of the cord. They are the largest cells found in the cord, being 30 to 70  $\mu$  across and up to 100  $\mu$  long. They have from 3 to 20 dendrites and axons (of from 8 to 18  $\mu$  diameter), a large central nucleus, and their cell bodies are filled with large "NissI bodies". The cells tend to be largest in the areas of the cervical and lumbar enlargements, for these areas of the cord send axons to the distal extremities to innervate skeletal muscle.

# (b) 🎖 Motoneurones and Renshaw Cells

Spread among the large a motoneurones are smaller neurones with finer axons, the & motoneurones, which supply the muscle spindle intrafusal fibres. These receive impulses travelling down the reticulospinal, and perhaps the vestibulospinal and rubrospinal, tracts. Also present are Renshaw



11

Fig. 3. Diagram of a cross section of the human spinal cord at an upper thoracic level. The descending fibres are organised into tracts, indicated here by dotted outlines.



Fig. 4.

Diagram of a cross section of the human spinal cord, showing grey and white matter. The ventral horn of grey matter is organized into motor muclei, as indicated. Also illustrated is an a motoneurone, a motoneurone, and a Renshaw cell. cells, small neurones that receive connections from recurrent collaterals from the large a motoneurones. The Renshaw cell axons in turn synapse on the same a motoneurone cell body from which their recurrent collaterals derived.

12

#### (c) Organization into Motor Nuclei

The large anterior horn cells are organized into motor nuclei, such that motoneurones innervating flexor muscles are separated from those going to extensors, and those innervating the distal extremities are removed from those travelling to muscles on the trunk. This pattern is illustrated in Figure 4.

# (d) Motoneurone Axons

The myelinated axons of the a and  $\delta$  efferents comprise much of the ventral root of the spinal cord at each level. They proceed along their particular motor nerve to a muscle after the two roots of the spinal cord fuse. Roughly 2/3 of the fibres are of the a type. They are from 8 to 18  $\mu$  in diameter, and conduct at 50 to 110 m/sec. The other 1/3 are of the  $\delta$  type: they are from 3 to 8  $\mu$  in diameter, and conduct more slowly at 15 to 50 m/sec. (Kuffler, Hunt, Quilliam, 1951). Conduction speed decreases slightly as the nerve gets more peripheral. (Magladery and McDougal, 1950).

- (6) The Neuromuscular Junction
  - (a) Morphology

The a motoneurone fibres, after branching repeatedly, terminate upon muscle fibres in small, flattened, oval expansions, the motor end plates, or neuromuscular junctions. They are from 40 to 60 µ long, 40 µ wide, and from 6 to 10 µ thick. The axon loses its myelin sheath as it approaches the muscle fibre, and is covered by neurolemmal sheath only. Details of the motor end plate have recently been worked out. (Reger, 1955, 1957, Robertson, 1959, 1960). The terminal part of the axon contains many mitochondria, vesicles, granular material, and tube-like bits of endoplasmic reticulum. It lies in a depression in the sarcolemma, the floor of which is irregular due to many infoldings of the sarcoplasma. A small gap separates the axon membrane and the sarcolemma. The whole ending is covered by a Schwann cell, which also has a gap between it and the axon.

# (b) The Motor Unit

Each motoneurone innervates a number of muscle fibres, due to its branching. The fibres supplied by the branches of one motoneurone axon constitute a "motor unit", and the size of this unit varies from muscle to muscle. In general, those muscles which do not have to contract quickly or accurately, such as soleus, have larger motor units. Muscles that require fine, rapid, control, on the other hand, such as the extrinsic eye muscles, have few muscle fibres per motor unit.

- (7) Skeletal Muscle
  - (a) Energy Conversion

Skeletal muscle is the machinery by which chemical energy is converted into thermal energy and mechanical work, after transmission of the nerve impulse occurs. The quantities and time relations of this conversion have been analysed in detail by A. V. Hill (1938, 1960). He made the fascinating observation, reported in his 1960 paper, that work may be absorbed by a muscle if it is stretched while actively contracting, and the chemical processes of activity may be reversed. The muscle is in effect acting as a storage battery for energy, which can be released later. This of course adds greatly to the efficiency of, for instance, leg muscles while running.

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#### (b) Mechanical Characteristics

The mechanical characteristics of skeletal muscle are still being analysed, and are very complex. For instance, force and velocity of contraction are inversely related in a non-linear fashion. (Fenn and Marsh, 1935, Katz, 1939, Wilkie, 1950). The simplest mechanical model must involve at least an active, contractile, component, and a passive, elastic, component, in series. (Wilkie, 1956). It is important to know the characteristics of a particular muscle under varying conditions of load, speed of contraction, and form of contraction (how fast the contraction builds up, how long it lasts, and how quickly the muscle releases). Only then can the neural component be separated from the inherent mechanical component of a voluntary contraction. As yet, suitable engineering studies of human muscle are too incomplete.

# (c) Microstructure

The gross structure of muscle has been known for many years, consisting basically of bunches of parallel muscle fibres (cells) wrapped up in fibrous sheaths. Each fibre can be from 1 to 40 mm. in length and from 50 to 100 µ or more in diameter. The fibre contains parallel myofibrils of from 1 to 2 μ diameter. They are surrounded by sarcoplasm and both are enclosed by the sarcolemma. The myofibrils are striated, and so placed that the muscle fibre appears to have alternate light and dark bands running entirely across it ("light" and "dark" here refer to the appearance when focussed slightly below the fiber viewed, with a low - intensity light source). The dark band contains a highly refractile material that makes it birefringent (anisotropic) and hence it is called the A band. The isotropic light area is called the I band. The centre of each A band is less dark, and is called the H band. A dark Z line is the final structure that can be seen with the light microscope; it bisects the I band. The unit of muscle consisting of the part between two Z lines is called a sarcomere. This is summarized in Figure 5.

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#### (d) Ultrastructure

More recently, the ultrastructure of muscle has been worked out. (Huxley, 1957, 1963). The myofibril was found to consist of parallel and overlapping filaments of two sorts. "Actin" filaments are the thinner of the two types, being 65 Å in diameter as opposed to 110 Å for myosin. They extend out in each direction from the Z line and end part way through the A band (at the beginning of the "H" zone). "Myosin" filaments lie across the width of the A band. It is the overlapping of these two types of filaments that causes the darker edges in each A band. The arrangement of filaments as seen in longitudinal section of one myofibril is diagrammed in Figure 6, and can be compared to Figure 5.



16

### Fig. 5.

16

The appearance of a single muscle fibre under the light microscope. The birefringent "A" band appears dark, and the non-birefringent "I" band appears light, when focusing slightly below the fibre with a low intensity light source. The "A" band is split by the lighter "H" zone, and the "I" band by the dark "Z" lines. The unit of muscle fibre between two "Z" lines is defined as a sarcomere.



# Fig. 6.

Diagram of a myofibril taken from humal skeletal muscle. The "A" band is seen to consist of parallel myosin filaments, and the "I" band of parallel actin filaments. These two complex proteins interdigitate in a sliding fashion. another is highly symmetrical, with each myosin filament surrounded by six actin filaments, and each actin surrounded by three myosins. A cross-section of part of a single myofibril is shown in Figure 7. Also shown is the very fine microscope section that would produce the picture of Figure 6.

17

The arrangement of the filaments relative to one

Myosin filaments are spaced from 500 to 550 Å apart. They are single-stranded proteins, and have small "bridges" connecting with the same actin filament about every 435 Å. (Each has bridges to six actin filaments about it.) Actin is a more complicated protein. It consists of two monomers in the form of an intertwined double helix, with the two strands 55 Å apart, and the pitch of the helix 410 Å. It connects (via the myosin "bridges") with one of the three myosins about it approximately every 145 Å. (Hanson and Lowey, 1964).

The slight difference in the length of the repeating segment in actin (410Å) and myosin (435Å) appears to be a real one (Huxley, 1963), and makes the system more complicated and harder to visualize. However, it could have a significant function in making sure that there are always some bridge sites on myosin that do not have to go more than a fewÅ to link up with suitable sites on actin. The cross bridges are the actual contractile mechanism, as it is by their shortening that the actin and myosin filaments are pulled along beside each other, interdigitating in a sliding fashion.

(e) Activation and Contraction

Davies (1963) visua lizes the system as follows: Ca<sup>++</sup>



Diagram of a cross section of a myofibril. The systematic arrangement of actin and myosin filaments is demonstrated. The phase and thickness of the longitudinal section used to derive the electron microscope picture of figure 6 is also indicated.

18

. S	Contraction Time (msec.)	Fusion Freq. (stim./sec.)	tetanus twitch
Soleus	(05	32	3.44
Rectus(eye)	7.5	350	10.7

Table 1.

Fig. 7.

A comparison of the mechanical properties of slow and fast muscle fibres. Soleus is a representative slow muscle, and an eye rectus muscle is a typical fast type. Data from Cooper & Eccles (1930). is released from the sarcolemma and endoplasmic reticulum when the muscle is activated by a nerve impulse. It links actin and myosin at suitable sites for a bridge between them. Due to the neutralization of an electrical charge on bound ATP of the cross bridge by the Ca<sup>++</sup>, the bridge spontaneously contracts to an a helix. This is the important mechanical event mentioned above. By the contraction, ATP and ATPase are brought side by side. A  $PO_4^{\equiv}$  is split off and this results in the bridge breaking. As ATP is reformed from ADP after the link breaks, a negative charge is regained and the bridge straightens again. The process can then repeat itself.

### (f) Fast and Slow Skeletal Muscle

While the fine structural contractile mechanism is similar in all types of muscle, the gross appearance and function of muscles varies considerably. I will not discuss smooth (non-striated) or cardiac muscle as these do not come under voluntary control. Skeletal muscle, however, can be divided into at least two broad types, with any intermediate type possible as well. This was originally pointed out by Ranvier (1873), and he classified the two fibre types as "red" and "pale". Red fibres had a more granular cytoplasm, more distinct longitudinal striations, and centrally as well as peripherally placed nuclei. He also stated that granular and clear fibres occur side by side in mammalian muscle. This was confirmed in flexor muscles in man by Gordon and Phillips (1953). Hess and Pilar (1963) went further in differentiating the two muscle types, in this case in the extraocular muscles of the cat. They stated that slow fibres had a less well defined sheath than fast ones. Slow fibres tended to have multiple nerve endings on them, while the fast ones had a single end plate per fibre. There was no propagation of excitation along the slow muscle fibre and the strength of contraction was proportional to the number of junctional potentials. By contrast, impulses were propagated along the fast fibres, and they responded with a typical all-or-none contraction.

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Cooper and Eccles (1930) added to the work of Ranvier, using soleus as a slow muscle and a rectus muscle of the eye as a representative fast muscle. Part of their data is shown in Table 1. The specialization of a rectus muscle to perform quick movements is quite obvious. Anderson and Sears (1964) used individual fast and slow motor units of intercostal muscles to confirm the above. They found the twitch tension of fast fibres to be greater than that of slow fibres. They also found the slow muscle contraction time to be 45 msec., compared to 28 msec. for fast muscle. Buller et al. (1960) derived a figure of 27 msec. for fast muscle from a pool of his values. Buller and Lewis (1965) and Wells (1965) partly explained the differing behaviour of slow and fast fibres. They showed that the active state plateau of slow fibres was longer, thus a slow muscle has a lower initial rate of decay of its active state, though it later falls at the same rate as fast muscle. The smaller rate constant in slow muscle produces a conservation of energy which could explain its increased capacity for maintained activity.

Several investigators became interested in what caused the differences between slow and fast skeletal muscle. Eccles (1944) reported that both disuse and tenotomy would cause muscular degeneration, and that more occurred in slow muscle than fast if there was no motor innervation. 20

Buller, Eccles, and Eccles (1960) hypothesized that a muscle's innervation controlled whether it became a fast or slow type. It had nothing to do with the frequency of discharges, but perhaps was due to a released chemical. Vrbova and Associates took up the story next. (McMinn and Vrbova, 1962, Vrbova, 1963a, Vrbova, 1963b). A careful histological study showed extreme degeneration of slow muscles and little of fast muscles after tenotomy. Slow muscle was shown to lose its spontaneous activity on tenotomy, while the pattern of fast muscle activity was unchanged. Soleus was shown to become a faster muscle after tenotomy, and its increase in twitch speed was apparently due to fewer nerve impulses. Vrbova hypothesized that excess use or load of a muscle caused it to become slower. Close (1964) showed that in the rat, all limb muscles are slow at birth, and as age increases, some become fast by an increase in speed of shortening. Actually, all rat muscles increased their speed of shortening, but the "fast" ones increased it more. Buller and Lewis (1965) doubt, however, that slow muscle can turn into fast muscle. They did show, nevertheless, in the rabbit, that contraction time does gradually fall off after tenotomy.

- (8) The Muscle Spindle
  - (a) Structure

Regardless of whether they consist of primarily fast or slow fibres, all skeletal muscles contain specialized sensory endings called muscle spindles. They were probably first described by Hassall in 1851

21

(quoted in Ruffini, 1898). The first good histological description was by Weismann (1861), followed rapidly by Kolliker (1862), and the end organ was first described as a spindle by Köhne (1863). Sherrington devoted considerable energy to examining muscle spindles in all parts of the body shortly after this. In 1894 (Sherrington, 1894), he described the end organs as fusiform and enclosed in fibrous capsules. They were from 80 to 200  $\mu$  in diameter and from 0.75 to 4 mm. in length. He was the first to use the term "intrafusal fibres" to denote small muscle fibres that he found inside the spindles, and pointed out that the nuclei of these fibres tended to cluster near their centres. Ruffini (1898) produced a series of complete and excellent drawings of the histology of muscle spindles, and these, along with the work of Cajal at about the same time (Cajal, 1899), remained the definitive work on the spindle structure until this decade and the work of Boyd and others.

#### (b) Location

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Sherrington (1894) was able to find spindles in all muscles that he examined, except those of the eye and the tongue. The situation in the tongue has been confusing, although spindles of a sort probably are present. Boeke (1917, 1927) found them only in tongue muscles attached to the hyoid, while Langworthy (1924) said they were numerous in the tongue. On the other hand, Carleton (1938) and Weddell (1940) felt they weren't present at all. In the case of the eye muscles, an eventual concensus of opinion was reached. Sherrington made another histological attempt at finding the spindles he felt should exist in the extraocular muscles in 1897 (Sherrington, 1897), but failed. However, Buzzard (1908) reported seeing spindles in them some years later. Tozer and Sherrington (1910), in a study of afferent nerves from the eye muscles, found peculiar receptive spindles in these muscles. Sherrington also later introduced experimental evidence that the function of spindles at least was present in them. (Sherrington, 1918). Definite histological proof that they existed was finally supplied by Cooper and Daniel (1949), along with a convenient explanation of previous failures. They said stretch receptors were not found in eye muscles for a long time, as they are grouped mainly near the proximal end of the muscle, while end plates are mainly in the middle of it. Conclusive electrophysiological proof of spindle function in eye muscles was provided by Cooper, Daniel, and Whitteridge (1951).

23

In general, then, spindles are found in all skeletal muscle. They occur in larger numbers in muscles that consist largely of slow ("red") fibres, such as soleus in the leg, and in lesser numbers in predominantly fast ("pale") muscle, such as gastrocnemius, or fine muscles of the hand. (Cameron, 1929, Hagbath and Wohlfart, 1952, Eldred et al., 1962). Swett and Eldred (1960) showed that contractions of soleus are slower, more sustained, and have a lower threshold than those of gastrocnemius. They suggest this is due to the larger number of spindles in soleus producing a stronger afferent signal to soleus motoneurones than that received by gastrocnemius motoneurones from its more limited receptors. The significance of the higher number of stretch receptors in slow muscle is thus obvious, for the slow muscles are those that maintain a steady posture, and the muscle spindle is an excellent length transducer, especially able to feed back the length of a postural muscle to the motoneurones controlling it.

(c) **X** Efferent Innervation of Spindles

As mentioned previously,  $\delta$  motoneurones originate in the ventral horn of grey matter of the spinal cord, along with a motoneurones. They consitute about 1/3 of the total number of fibres in an efferent nerve, on their way to supplying the intrafusal muscle fibres. This was described by Eccles and Sherrington (1930), who showed two distinct groups of fibres, according to diameter. Laksell (1945) was the first to call them "efferent  $\delta$ " fibres. Hunt and Kuffler (1956) said that all type A stretch receptors (muscle spindles, Matthews' classification) have a  $\delta$  innervation. One fibre goes to several spindles and several fibres go to one spindle, producing much redundancy and spreading of the load. Hay (1901) showed that slow muscles receive more small nerve fibres than fast ones. This is natural, since slow muscle has more spindles, though he could not explain it this way.

#### (d) Spindle Afferents

Before describing the fine structural details of muscle spindles, including their afferent and efferent nerve endings as currently understood, the loop between them and the a motoneurones must be closed. Afferent fibres of several types from the spindle have been described. Matthews (1933) classified the afferents, according to their physiological responses, into types  $A_1$ ,  $A_2$ , B, and C.  $A_1$  and  $A_2$  came from muscle spindles, B from tendon organs, and C from fascia or elsewhere. The  $A_2$  and B fibres were of similar
size and conduction velocity, while the A<sub>1</sub> fibres were smaller and slower. Hunt (1953) took a combined physiological and histological approach and showed that the distribution of stretch-activated afferent fibres corresponded to groups I and II of the histological spectrum. The afferents from tendon organs were confined to group I (he called them IB), as were some spindle afferents from primary spindle endings (group IA). Spindle afferents from secondary spindle endings fell in group II. He found the relative numbers of afferents to be : IA - 55, IB - 40, II - 101. Table 2 summarizes Hunt's and Matthews' classifications of muscle afferent fibres, and includes synonomous names for the endings from which they originate for the sake of completeness. These will be described later.

15

There is no monosynaptic excitatory pathway from the primary afferent fibres (at least) to the 8 motoneurones. (Hunt and Paintall, 1958). Only the a motoneurones receive direct connections.

Figure 8 summarizes tha paths to and from the muscle spindle.

The feedback nature of the pathways, a very important functional point, is now quite evident. However, before considering how the loop functions, some more details of spindle histology must be described.

(e) Spindle Histology

Boyd (1962) has furnished us with the best recent description of this end organ. He describes two types of intrafusal fibres. Nuclear bag fibres are less than 1/2 the diameter of extrafusal fibres and have their nuclei packed together in a bulging central section. There are usually two

Hunt	Matthews	Size (m)	Cond. Speed ( <sup>m</sup> /siec.)	Anges Endings
IA	Az	12-20	70-110	annutospiral nuclear big
I	A,	4-12	15-70	2° flower spray mystube
IB	В	12-20	70-120	Golgt tenden ørgen

<u>Table 2.</u> Classification of muscle spindle afferent nerve fibres. They form 3 groups, distinguished by fibre size, conduction velocity, and the type of nerve ending. The designations given each group by Hunt (1953), and Matthews (1933), are indicated.



# Fig. 8.

26

Diagram to illustrate the afferent and efferent nerve supply of a typical skeletal muscle and a muscle spindle in it. Higher centres can excite the  $\alpha$  or  $\mathbf{X}$  motoneurones. The  $\alpha$  motoneurones cause the muscle to contract while the  $\mathbf{X}$  motoneurones cause a contraction of the poles of the spindle, which in turn causes  $\alpha$  motoneurone excitation via type IA and II afferent fibres. Tendon organs send back inhibitory impulses via the IB afferents.

per spindle. They practically never branch. They contain numerous myofibrils, which are uniformly distributed in cross-section, and relatively little sarcoplasm. Several small  $\aleph_1$  fibres end in a number of discrete motor end plates on the nuclear bag fibres. The innervation is of both ends of the fibre, which are contractile, not the non-contractile centre section. Nuclear chain fibres are about 1/2 the length and diameter of nuclear bag fibres and have a single row of central nuclei in the equatorial region. There are usually four per spindle. They have fewer myofibrils per unit area, irregular in size and distribution, and relatively more sarcoplasm. Several very small  $\aleph_2$  fibres end in a network of fine axons and endings on most regions of the nuclear chain fibre other than the equatorial. All spindles receive  $\aleph_1$  and  $\aleph_2$  innervation.

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Boyd says each spindle has one group IA afferent from a primary sensory nerve ending, and from zero to five group II afferents from secondary nerve endings. The 1<sup>°</sup> endings are on both nuclear bag and nuclear chain fibres, while the 2<sup>°</sup> endings tend to lie on nuclear chain fibres. Primary endings occur near the equatorial region, while secondary endings are more towards the ends of the fibres.

A further comment in Boyd's article is that spindles in tonic muscles have more secondary sensory endings, and motor nerve fibres and endings, than those in other muscles. He felt that nuclear chain intrafusal fibres are slower than nuclear bag fibres which in turn are slower than extrafusal fibres. Matthews and Westbery (1965) said that the spindles of frog muscle contain both fast and slow intrafusal fibres. They stated that stretch

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to a muscle does not tend to increase the sensitivity of the ending to dynamic stimuli while stimulating fast fibres, but does greatly increase the sensitivity if a slow fibre is stimulated. That is, slow fibres cause an increased response to dynamic stimuli, while fast fibres do not. Bessou and Laporte (1965) went further by stating that the nuclear chain fibres and their  $\aleph_2$  innervation have a static function, while the nuclear bag fibres and their  $\aleph_1$  innervation have a dynamic function. Bessou, Emonet-Denand, and Laporte (1963) have also traced a motoneurone fibres and found that while all went to extrafusal fibres, some of the smaller a fibres also had a specific excitatory action on some spindle primary endings, i. e., some small a fibres innervate intrafusal fibres as well. Not all spindles get an a innervation, however. They further speculated that slow a fibres may greatly increase the sensitivity of primary endings to dynamic stimuli.

The histology of the spindle as described by Boyd (1962) is diagrammed in Figure 9.

Most of the above detail is considered to be correct. However, certain features of the motor innervation have been disputed by Barker (1965). He suggests that the diameter of  $\delta$  fibres is of no importance (Boyd said  $\delta_2$  fibres were smaller than  $\delta_1$ ), and that it is how and where they terminate in the spindle that matters. While he says there are two kinds of motor endings, he feels neither is specific to one type of intrafusal fibre. He is of the opinion that static fibres end in the spindles as "end plates" and dynamic fibres as "trail endings". Granit (1965) has summarized the eventual common ground that was attained by Boyd and Barker. The terms  $\delta_1$  and  $\delta_2$  no longer



# Fig. 9.

Diagram of a muscle spindle and its innervation. Both nuclear chain, and nuclear bag fibres receive a  $\mathbf{X}$  efferent supply, and in turn, send impulses back to the cord viat type IA and type II afferent fibres.

apply and should be abandoned. There are two types of **X** fibre, recognizable by their "plate" endings and "trail" endings. Apparently, static fibres end as plates, and dynamic fibres as trails. The distribution of endings is as yet unsettled.

# (9) <u>The & Loop</u> (a) Spindle Function

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This, then, is the structure of the "& loop " system in man. What is its function, and how does it carry it out? Spindles do not contribute to conscious proprioception. This has been amply demonstrated by Provins (1958) and Merton (1964) (quoted in Matthews, 1964). The earliest approach to the problem was the study of the phenomenon of the tendon jerk, especially at the knee. Sherrington (1892) traced the pathway of the knee jerk and described it in detail. He repeated this description in 1893 and added that dorsal root section would abolish the reflex. He also observed that the most efficient mode of excitation of the afferent fibres from the muscles involved appeared to be the mechanical (the "myotatic"). Hoffmann (1919) then showed that, after a tendon jerk, there was a complete absence of action currents in a muscle for about 1/20 of a second.

# (b) The Stretch Reflex

The stretch reflex as we know it was first described in a classical experiment by Liddell and Sherrington (1924). They used an arrangement whereby the quadriceps of a decerebrate but otherwise intact cat could be suddenly stretched, and the force exerted by the muscle measured. They found that stretching the muscle evoked a contraction in it, which was abolished if the nervous supply of the muscle was not intact. They stated it was "a reflex and purely proprioceptive contraction, with its receptors lying in the fleshy region of the muscle". Slow as well as fast stretch would result in the reflex, and its magnitude was dependent on the degree of stretch. The contraction could be easily inhibited by other antagonistic reflexes.

31

Denny-Brown (1924) noted that the soleus in cats gave a better stretch reflex than the gastrocnemius, though both muscles respond to a passive stretch in this fashion. (We now know that soleus, as a "slow" muscle, has more muscle spindles and a larger afferent representation.) He made the correct statement that the (passive) stretch reflex is essentially spinal in nature; however, he also said that stepping is also essentially spinal in nature, and this is probably not so.

In 1926, Adrian described an amplifier and capillary electrometer with which he obtained some of the first observations on action potentials in sensory nerve fibres due to end organ stimulation. This included muscle stretching. Later in 1926, Adrian and Zotterman went further by isolating a single end organ (muscle spindle) in the sterno-cutaneous muscle of the frog by cutting successive bits and strips from it until only one remained. They stretched the muscle preparation, and found the afferent discharge was regular, with a frequency that was roughly proportional to the load, and inversely proportional to the time that the load was sustained.

The work of Adrian and Zotterman (1926) was with passive stretch to a muscle. Cooper and Creed (1926, 1928) caused a muscle

to actively contract and examined the "stretch reflex action currents" during the contraction. They found that these disappeared during the contraction, in the muscle itself, and also in its synergists. This latter fact was taken to be due to inhibitory impulses from the muscle.

31

Fulton and Pi-Suner (1928) then speculated as to the function of the muscle spindle and tendon organ. They based their ideas on the fact that the spindle was in parallel to extrafusal fibres, and on the presence and absence of a silent period following a jerk and passive stretch to a muscle, respectively. They stated that the spindle must be the seceptor for the knee jerk and stretch reflex. The tendon organs should be tension recorders, and may produce reflex inhibition of the muscle. They were later to be proved entirely correct, though at the time, there was some opposition to their ideas. Denny-Brown (1928) feit that muscle spindles responded to muscle excitation and not to passive stretch. He felt the tendon organ was the only end organ responsive to stretch; within several years, it was shown conclusively that he was incorrect.

# (c) "Fatigue" of Muscle Spindles

Bronk (1929) added to the knowledge of spindle response by studying their "fatigue" due to sustained tension. He demonstrated a rapid adaption of the end organ, followed by a more gradual decrease in the frequency of their impulse discharge.

(d) Type A<sub>1</sub>, A<sub>2</sub>, and B Spindle Afferents

It remained for B. H. C. Matthews to perform his

definitive experiments on spindle function between 1929 and 1933. These first required the development of his "oscillograph" (Matthews, 1929), so that he could record rapidly fluctuating electric potentials. He then examined the afferent response due to a static load, using a preparation of frog muscle with one spindle in it. (Matthews, 1931a). He found that the afferent nerve impulse frequency was proportional to the log (load). With sudden loading, a very high frequency discharge occurred, lasting only a short period of time. The response also varied with temperature. He then went on to examine the afferent response during active contraction of the muscle. (Matthews, 1931b). He found that, if slight initial tension were exerted on the muscle, a twitch of the muscle caused a pause in afferent impulses, followed by a transient imcrease in afferent impulse frequency . Tetanizing the muscle produced no afferent discharges, but if the stimulus to the motor nerve was supramaximal, the pause in the afferent impulses was sometimes obliterated (as  $\checkmark$  efferents were stimulated). He followed his results by describing the spindle as a self-regulating tonus mechanism feeding back information about mechanical events in the muscle. He explained the silent period after a tendon jerk as being due to a decreased response of the muscle spindles.

33

Matthews continued to work on the responses of afferent fibres from muscle, and in 1933 presented a classification that is still valid. (Matthews, 1933). Only the three types of fibres coming from a muscle or its tendons will be mentioned here, though he went beyond this. Type A<sub>1</sub> fibres are relatively small, respond with a low threshold, and show the typical response to passive stretch (increased firing plus adaptation) and muscle contrac-

tion (a pause in firing) described previously. (Matthews, 1931a, 1931b). Type  $A_2$  respond in a similar fashion, but are large afferent fibres. They also have a higher threshold, and will increase their firing frequency upon supramaximal motor nerve stimulation, unlike type  $A_1$ . Both  $A_1$  and  $A_2$  fibres come from the muscle spindle. Type B fibres are large, like type  $A_2$ . They respond to stretch or contraction with an increased firing frequency, and they have a much higher threshold. They originate in the Golgi tendon organs.

#### (e) Spindle Efferent Innervations

With this complete work of Matthews, attention now turned to the efferent side of spindle innervation. The division of motor fibres into two groups according to diameter was by this time well established. O'Leary, Heinbecker, and Bishop (1935) said that this indicated the groups had different functions, and suggested that the smaller group might be motor to the muscle spindles.

It was the work of Leksell (1945) that proved the above three to be correct. He showed that the threshold of the small fibres to electrical stimulation was 3.9 times that of the larger fibres. He also made the important discovery that controlled pressure upon the intact motor nerve could selectively block the larger fibres. Using this fact to great advantage, he showed that the smaller fraction did not contribute to the contraction of the muscle, but small fibre stimulation increased the sensitivity of muscle afferents. Stimulation of larger fibres did not increase afferent sensitivity. He measured conduction rates as 20 to 38 m./sec. for the small fibres, which he named "efferent &", and about 100 m./sec. for the a fibres.

#### (f) Further Studies of Spindle Function

The basic mechanism of the spindle and its afferent and efferent nerve supply had thus been worked out by 1945. Merton (1950, 1951) showed a monosynaptic electromyographic response and then a 100 msec. silent period in the e.m.g. following a tendon tap to the hard muscle from which he was recording. (A monosynaptic response returns to the same muscle or group of muscles of origin. (Lloyd, 1943, Eccles, Eccles, and Lundsberg, 1957)). He also extended Matthews' theory of the servo properties of muscle spindles at this time. Huntand Kuffler (1951a) continued Leksell's work by again showing that stimulation of the efferents caused an increase in the firing rate of the spindles. They added that it decreases if the main muscle contracts, especially if allowed to shorten. (This follows from the fact that spindles lie in parallel to extrafusal fibres.) They attempted to determine the effect of muscle contraction on each of Matthews' type of receptors  $(A_1, A_2)$ and B), but were only successful in finding two types, A and B, whose fibres conducted at equal rates (About 60 to 125 m./sec.). (Hunt and Kuffler, 1951b). They confirmed that A units decrease firing frequency during extrafusal contraction, while B units increase discharge frequency, and have a higher threshold. Hunt (1951) showed that in many reflexes, (e.g., the flexor) an increase in efferent small nerve (X) activity to a flexor muscle occurred together with a parallel increase in a activity. Both a and  $\,{f arsigma}\,$  activity to the flexor muscles were inhibited in crossed extensor reflexes. In this case, the  $oldsymbol{\delta}$  fibres to the extensors discharged at a higher frequency, and had a lower threshold to

reflex stimulation.

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Granit and Strom (1951, 1952) now showed that the monosynaptic response decreased if a muscle were de-efferented, saying that this was due to a decreased tonic influence on the muscle spindles from the efferents. They also showed that this effect disappears if the muscle is under high initial tension. Hunt (1952) showed that a tetanic contraction of gastrocnemius inhibited a monosynaptic response in the muscle. Henneman and Hertz (1953) showed that the monosynaptic response is facilitated in flexor muscles by placing an initial static load on the muscle. They also showed the reverse was true in extensor muscles. This work by several researchers, between Leksell's paper of 1945, and 1953, provided the basis for Hammond, Merton, and Sutton's paper of 1956 in which the complete modern servo concept of muscle spindle function was enunciated.

Meanwhile, Merton explained why Hunt and Kuffler (1951b) did not find two groups of muscle afferents according to velocity by showing that the smaller group were very easily destroyed during the dissection required. (Merton, 1953). He did find some slow-conducting afferents and thus confirmed Matthews' work of 1937. It was not long after this that Hunt was also able to find them, and describe his classification into types IA, IB, and II, as given previously. (Hunt, 1953).

#### (g) The Functional Stretch Reflex

Hammond, Merton, and Sutton, (1950), published a paper on the "nervous gradation of muscular contraction" in which they described

how a muscle controls its strength of contraction to allow for the task it is performing. They described the spindle and  $\delta$  loop as a length servo, a "closed-loop mechanism using negative feedback from the spindles to maintain a constant muscle length", that would automatically compensate for changes in load or for fatigue. Beyond this, it is also a "follow-up length servo", as it can be set rapidly to maintain or change any muscle length by  $\delta$  biassing. However, they also suggest that direct a activation of muscle can occur in the case of sudden, gross, movements.

They demonstrated the functional stretch reflex in the biceps of the human arm, and showed it to have a latency of from 60 to 80 msec. following a sudden force extending the elbow, which the subject resisted. It consists of a burst of e.m.g. activity, rather unsynchronous from one pull to the next. It is always preceded by a monosynaptic, diphasic, e.m.g. response representing the tendon jerk. This early response had no effect on the force exerted by the muscle, however. The authors hypothesized that the monosynaptic response is an unphysiological result of an accidental overload of the feedback pathway, before Renshaw inhibition can control it (in 2 to 5 msec.). (Renshaw (1941) showed recurrent collaterals from axons running back to the ventral horn cell from which that axon originated and inhibiting the motoneurone for a period of from 40 to 50 msec.).

The concepts of the above paper were later expanded and a more quantitative analysis of the loop performed and reported on in a paper by Hammond (1960).

# (h) Further Studies of **X** Loop Function

38

Several more details of  $\mathcal{V}$  loop function have been worked out recently. Hunt and Paintall (1958) showed that, in comparison to a motoneurones,  $\mathcal{V}$  motoneurones recover quicker and discharge at a higher rate. They also tend to show repetitive discharges after a single afferent volley. Jansen and Matthews (1962) have investigated the control of static and dynamic muscle spindle response by fusimotor activity. They showed that it increases the static response of secondary endings, may increase or decrease the dynamic response of primary endings, and may independently control the static response of primary endings, possibly by separate control of the two types of intrafusal fibre. An interesting research trick was developed by Hagbarth and Eklund (1965) when they showed that rapid (400/sec.) small amplitude stretches to a muscle selectively stimulates the primary endings only. And, Granit (1966) used a method to knock out  $\mathcal{V}$  afferents selectively to show that IB fibres act constantly in an inhibitory manner (not just if the muscle is overloaded). They are usually overwhelmed by the IB fibres, however.

Magnus (1926) concluded that posture was the result of the cooperation of a great number of reflexes, including those from the spine, brain stem, cerebellum, and basal ganglia. Later, Granit and Kaada (1953) concluded that the  $\checkmark$  efferent system is tonically activated from central regions and in its turn controls the tonic activation of the muscle spindle afferents. Boyd (1964) wrote that the central nervous system can control the amount of velocity sensing by spindles. He felt, however, that these receptors acted

mostly at the spinal level, not at a cortical one. Matthews (1964) acknowledged that  $\checkmark$  motoneurones were readily influenced by local reflexes, and c.n.s. stimulation. Tokizane and Shimazu (1964) felt that as you go up the phylogenetic scale, there is less spinalization and more cortical control of movement, centralization being largely a fine regulatory mechanism. Higher nervous control of the  $\checkmark$  loop is becoming more and more important in our understanding of the control of voluntary movements. A further look at the function of this very complex and as yet poorly understood area is now in order.

# (10) Higher Control of the $\delta$ Loop

# (a) The Reticular Formation

Shimazu, Hongo, and Kubota (1962) showed that by varying the strength of stimulation to the reticular formation, flexor motoneurones could be excited and extensors inhibited. The opposite could also occur. This is suggestive of at least two centres in the reticular formation, one "flexor positive" and "extensor negative", and the other "flexor negative" and "extensor positive". Part of the anatomical basis of these centres has been worked out, and a diffuse bulboreticular inhibitory system described. (Magoun, 1944, Magoun and Rhines, 1945, 1946, Reimer and Magoun, 1947). That this was not the only area active in X control was shown by Smith (1945), Kaada (1951), and Hodes, Peacock, and Heath (1951), when they all demonstrated inhibition of stretch reflexes and tonus on stimulation of the anterior limbic gyrus.

The reticular formation, from the diencephalon down to the spinal cord, does more than this, providing the **b** system with a collecting network. This included parts of the bulbar reticular formation, the pontile tegmentum, the central grey matter, and the tegmentum of the mesencephalon (Magoun, 1944, Rhines and Magoun, 1946), the ventral diencephalon (Murphy and Gellhorn, 1945), parts of the midline and intralaminar group of thalamic nuclei, and certain of the specific thalamic nuclei as well. (Jasper, 1949, Austin and Jasper, 1950, Peacock and Hodes, 1951), (Granit, 1955).

## (b) The Cerebellum

The cerebellum is a major area of control of the system. This was demonstrated clearly by Granit, Holmgren, and Merton (1955), who showed that cooling or ablation of the anterior lobe of the cerebellum increased discharges of the a motoneurones, while decreasing X activity. This is suggestive of different pathways to a and X motoneurones. Granit (1955) showed that anemic decerebration also increases a activity. However, he also showed that decerebration by trephire increases X activity. **G**laser and Higgins (1965) added an interesting concept of cerebellar function. They felt that it caused muscle tension to lead the stretch response in phase. This would tend to stabilize the system and reduce an inherent tendency to oscillate owing to time delay. The cerebellar effect would provide an additional fine adjustment for the timing of motor activity.

# (c) The Cerebrum

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It is becoming more evident that the cerebrum has a function in control of the  $\checkmark$  loop. Eldred, Granit, and Merton (1953) showed that cerebral stimulation could increase  $\checkmark$  activity. Granit (1955) showed the different effects on  $\checkmark$  activity of different types of decerebration, as described. Oscarsson (1965) finally demonstrated a projection of IA afferents to the cerebral cortex. This tract travels via the cuneate nucleus and ventrobasilar thalamus to an area in front of the post-cruciate dimple, outside the classical sensory cortex. It is not a conscious input, and may be a feedback used to control movements elicited from the cortex.

# (d) Clinical Correlation

In 1898, Sherrington described the condition known as decerebrate regidity. He noted that it was a type of extensor spasm and was largely determined by centripetal impulses coming from the limb in question. It could be inhibited by stimulation of various areas of the central nervous system and various peripheral nerves. Today, we can add that it is due to an imbalance of  $\mathbf{X}$  control from centres in the reticular formation. The extensor positive, flexor negative centre apparently dominates when cerebral control is interrupted. There is still no certain explanation for spinal shock, that immediate flaccidity following spinal cord transection. It is felt that it is the effect of the sudden blocking of down-going tracts. (A second cut lower down has no effect.) Later, spasticity develops, but whether it is due to Renshaw cell malfunction or to increased afferent activity due to sprouting is not known.

#### (11) The "Long-Loop" Reflex

One recent development in the field of muscle control remains to be discussed. This is the long loop reflex from the spinal cord to the brain stem and cerebellum and back. This was summarized by Eccles (1966). It has been shown that a volley in a cutaneous nerve will evoke a reflex response that comes considerably later than the early and well known flexor reflexes. It travels to the pontine and bulbar reticular formation and back down the cord, exciting motoneurones at all levels and on both sides. Using "H-reflex" testing of the gastrocnemius-soleus muscles in man, with conditioning and test stimuli to IA afferents from these muscles, the excitability of motoneurones to these muscles could be measured and the effects of early and long-loop reflexes evaluated. It was found that a total suppression of excitability in the a motoneurones occurred for 60 msec., with almost full recovery at 250 msec., but a further suppression occurred at 400 msec., before complete recovery at 1200 msec. The intercurrant recovery, beginning at 50 to 100 msec., and being maximal at 200 msec., is apparently superimposed on a gradual underlying recovery, and is likely due to a long loop reflex. A similar response has been obtained using sudden dorsiflexion of the ankle combined with H-reflex testing by Yaborikova, Provini, and Decardia (1966). The pathways of the long loop reflexes have been described in detail by Eccles (1965). The physiological significance of the long-loop reflexes in muscle control and in the occurance of spinal shock have not yet been fully explained.

### (12) Review Articles

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It can be seen that in the field of muscle control, it is difficult to draw a sharp line between the voluntary and involuntary. Also, the scope of the field is vast. It is therefore fortunate that a number of review articles have been written on the subject. These include Hinsey, J. C. (1934), Tiegs, D. W. (1953), Hunt, C. C. and Perl, E. R. (1960), Matthews, P. B. C. (1964), Barker, D. (1948, 1962), and Granit, R. (1965). The problem areas of this experimental study are arranged in this section in the form of five questions, raised by previous work reported in the literature, and by findings reported in this thesis. A similar division into five parts will be used in the sections entitled "Methods" and "Results".

#### Part I:

Although the afferent innervation of mammalian skeletal muscle is now known to comprise a complex balance of excitatory and inhibitory influences, sudden stretch of a muscle will usually cause an effective reflex opposition to that stretch. Thus, Hammond, Merton, and Sutton (1956) have demonstrated a functional stretch reflex in the biceps muscle of the human arm. It occurs after an apparently non-functional monosynaptic response to tendon tap (15 - 20 msec.), has a relatively fixed latency of from 60 to 80 msec., and is active long before the first possible voluntary response to light touch of the skin.

#### Question I:

Can a similar stretch reflex be demonstrated in the leg?

#### Part 2:

The presence of an apparently highly capable servo system to match muscle strength of contraction to muscle load has prompted many authors to assume this

is the basis of walking and stepping. Brown (1911) said: "A mechanism confined to the lumbar part of the spinal cord is sufficient to determine in the hind limbs an act of progression which is probably very nearly a normal one". He did qualify this, however, by saying that the phasing of the activity is probably central. Denny-Brown (1924) said that: "The stretch reflex and stepping are essentially spinal in mechanism". Boyd et al. (1964) said that muscle receptors function mainly at lower levels of the nervous system for organizing and controlling the execution of movements. However, the functional stretch reflex in the arm takes from 60 to 80 msec.; it will emerge in this thesis that it takes about 120 msec. in the leg. After the foot first touches the ground in a step, then, it will take at least this time before any functionally significant reflex muscle activity can occur. If this were his sole decelerative mechanism, a person stepping down one foot would fall another 14 inches after his toes touch before producing a functional response in the calf muscles. Since in these circumstances the heel does not normally hit the ground, some other mechanisms must be involved. Engberg and Lundberg (1962) showed e.m.g. activity in the extensors of the ankle occurring before landing from a stepping movement. An investigation by Battye and Joseph (1966) in the cat showed activity in soleus during stepping movements before contact with the ground.

#### Question 2:

Is the neuromuscular activity associated with landing completed before the functional stretch reflex can make any contribution?

## Part 3:

46

Glaser and Higgins (1965) suggested that the cerebellum adds a dynamic modification to the stretch reflex response, resulting in muscle tension leading the stretch response in phase. This phase advancing requires a cyclical pattern of movement if it is to be based on muscle spindle afferent signals. In Part 2, we considered only the response to non-repetitive single steps.

#### Question 3:

Is the pattern of neuromuscular activity associated with landing different for (a) a single step to the ground, and (b) repetitive landing, as in hopping at a constant rate, which would permit prediction of the moment of landing on the basis of muscle afferent information?

### Part 4:

If some form of prediction of the moment of landing is required, a timing error should result in an incorrect pattern of neuromuscular activity on landing, and hence, a fall.

#### Question 4:

What would the pattern of neuromuscular activity be if the moment of landing were totally unpredictable, such as in a sudden fall at an unexpected moment?

#### Part 5:

In order to present the fifth and last question, it is necessary at this point to

anticipate the results of an experimental inquiry into Question 4. These suggested a rapid reflex activation of the extensors of the ankle during a fall, possibly originating in the vestibular system. It is possible that in the case of steady hopping, vestibular influences are of comparable importance to the stretch reflex - cerebellar mechanism. Experiments to this point had showed a remarkable ability of the leg muscles to control the force exerted by the ball of the foot during a landing, regardless of height of step (and, hence, of velocity of landing). Single cells have been found in the vestibular nucleus that respond accurately to vertical linear acceleration only. Modulation of the monosynaptic stretch response can be shown due to rotational stimuli. And, decerebrate cats often show cyclical extension and flexion of their limbs when oscillated in a vertical, linear, sense. (Dr. G. Melvill Jones, personal communications).

#### Question 5:

Is the activity in a muscle contracting in an isometric fashion altered by subjecting a subject to rhythmic vertical accelerations?

48

A total of 23 human subjects were used in these experiments, most ranging in age from 20 to 25 years. Twenty-two were male and one was female, who showed no significant differences in her results. All were in good health at the time of the experiment, and had no history of neurological or muscular disorders.

In all cases, surface electromyograms obtained with Beckman skin electrodes were used to monitor muscular activity. The gastrocnemiussoleus group of muscles was considered as representative of the antigravity muscles of the leg, and was used throughout the experiments.

By careful electrode placement, it is possible to record what is primarily a soleus surface e.m.g. The prominent bulge of the calf muscles consists mainly of the bellies of the two heads of the gastrocnemius muscle. If the electrodes are placed just below and in line with the lateral and medial edges of this bulge, with the indifferent electrode in the midline between them, they lie over the lower part of the body of soleus, and a bit of the gastrocnemius tendon. Electrodes placed over the center of the bulge of the calf muscles overlie the gastrocnemius, which in turn is superficial to soleus. We have rather arbitrarily considered this to produce a gastrocnemius e.m.g., however, and are somewhat justified by the results as summarized in Figures 47 and 48. During stepping movements, the "gastrocnemius" e.m.g. started much earlier than the "soleus" e.m.g., so showing activity in the gastrocnemius when none was present in soleus. Also, the soleus e.m.g. was present after the end of the gastrocnemius e.m.g., demonstrating that the gastrocnemius electrodes were not picking up activity in soleus. This was confirmed more strongly by the results of repetitive hopping.

49

It has been shown by Sutherland (1966) that the potential moments about the ankle produced by the soleus and gastrocnemius combined are nearly six times the sum of the moments of the remaining muscles. Thus, in the normal person, the plantar flexion action of gastrocnemius and soleus overshadows that of the other plantar flexors. It has also been shown that the frequency of e.m.g. impulses is proportional to the electrical activity of the whole muscle (and is proportional to the integrated e.m.g., and the kinetic energy produced by the muscle in a voluntary contraction). (Bergstrom, 1959a, 1959b.) Using several methods to detect increases or decreases in the frequency of e.m.g. spikes, therefore, an attempt was made to answer the questions posed previously.

#### Part 1:

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Can a functional stretch reflex, similar to that described in the arm by Hammond, Merton, and Sutton, be demonstrated in the leg?

#### Apparatus

Eight subjects were used in the experiment. The gastrocnemius – soleus e.m.g. was recorded using Beckman surface electrodes, which were found to be free of noise or drift despite violent leg movements, if the inter– electrode resistance was below 2 K ohms, D.C. Scraping and cleaning of the skin at the point of application was of great importance. E.m.g. potentials of from 3 to 5 millivolts (peak to peak) were usually obtained during strong muscular contractions.

The force exerted upon the ball of the foot was recorded by means of an Endevco model 2104–1000 piezoelectric load cell mounted on a lever which was in turn hinged to a frame fixed to the leg. (Figure 10). The signal from the force transducer was amplified by a Kistler charge amplifier and displayed on an oscilloscope. The lever of the apparatus could be fixed relative to the frame, or it could be connected by rubber tubes so as to maintain a load on the calf muscles. Taps could be given to the Achilles' tendon by means of a simple aluminum bar and tapping hammer. The moment of a tendon tap was recorded using an Astatic microphone to display the sound produced by the hammer hitting the aluminum bar. The microphone could also be used to record the moment at which auditory cues were given to the subject. Arrangements were always carried out to minimize errors due to the transmission



51

Fig. 10. Apparatus used for generating and recording a functional stretch reflex in the lower leg. The leg was firmly fixed to a wooden frame, and the foot pressed against an aluminum plate that was attached by a hinge to the main frame. The ankle could be held at a right angle by a fixed support, or, if this were removed, the ankle could freely flex and extend. Constant dorsiflexing forces could be applied by means of elastics as illustrated. Access to the Achilles' tendon was through a hole in the wooden frame. The force exerted by the ball of the foot was continuously measured and recorded by means of a piezo-electric load cell, positioned, and heat-insulated, as indicated. time of sound in air.

52

In all experiment, a Krohn-hite low frequency oscillator was used to produce a 100 c.p.s. time base. This was calibrated using the oscilloscope to ensure maximum accuracy.

All information was displayed simultaneously on a Tektronix type 565 oscilloscope, and was photographed by a Shackman recording camera, passing a 35 mm. film by the 'scope face from 1 to 4.5 inches per second.

The force applied to the ball of the foot has been taken as being directly proportional to the tension in the Achilles' tendon. This implies that elasticity, etc., in all interconnections is negligible. As it may be shown that monosynaptic reflexes due to direct tendon tap, or a tap to the ball of the foot, have virtually identical latencies, this appears to be a valid assumption.

#### Procedures

Eight manoeuvres were requested of each subject at the time of experiment, and each was repeated many times. The manoeuvres were performed in a different order each time.

The subject was requested to plantar flex his foot as rapidly as he could when he heard a click by his ear.

He was requested to perform the same manoeuvre when the side of his foot was tapped.

He again twitched his foot after he felt a tap to his Achilles' tendon .

The above was repeated, but the elastics were used to put his

tendon under initial tension before tapping it.

He was requested to plantar flex his foot when the elastics were used to suddenly apply and maintain a dorsiflexing force to the foot. This is similar to the method used by Hammond, Merton, and Sutton (1956) to demonstrate the functional stretch reflex.

Each subject was asked to randomly twitch his foot, without taps of loading, to measure the delay between the e.m.g. and mechanical events in the muscle.

The monosynaptic reflex time was determined by tapping the Achilles' tendon, without any voluntary response from the subject.

Lastly, the monosynaptic reflex time was determined by tapping the ball of the foot, again, without a voluntary contraction.

#### Data Analysis

53

For purposes of data analysis, the film record was projected, and hence, greatly enlarged. It was then a simple matter to measure the time between the tap of auditory cue and the start of e.m.g. activity. In the case of random voluntary twitches, the time between the start of e.m.g. activity and the start of force buildup was taken.

Averages, standard deviations (S.D.) and standard errors (S.E.) were determined for each manoeuvre for each subject. Overall averages, S.D.'s, and S.E.'s were also calculated for each manoeuvre.

### Part 2:

Is the neuromuscular activity associated with landing completed before the functional stretch reflex can make any contribution?

#### Apparatus

Two separate groups of eight subjects each took part in this experiment. The gastrocnemius – soleus surface e.m.g. was recorded as before, and a microphone was again used to detect the instant the toes touched the landing platform. The soleus e.m.g. was also recorded in four of the first group of subjects. Subjects stepped down from wooden boxes constructed to be 5, 10, and 15 inches higher than the level of landing. In one subject, the angle formed by the ankle was continuously measured. A device was constructed (Fig. 12) consisting of metal plates fixed to the plane of the sole of the foot and that of the tibia, connected by a system of parallel rods. A potentiometer was mounted over the talo-tibial joint with its body fixed to the plate on the foot. The moving contact was fixed to the end of the parallel arm assembly, which followed the position of the tibia. This system responded to changes in the angle between the tibia and the sole of the foot, but was not attected by other movements, such as abduction of adduction of the ankle.

A special platform was built to record the force applied to the ball of the foot during the succeeding experiments. (Figure 11). The piezo-electric load cell, as previously described, was rigidly bolted to a 1/4 inch thick aluminum disc and was surrounded by a hard plastic sleeve as a bearing surface (as the gauze had a compressibility of  $8 \times 10^6$  lbs./inch, and so the



# Fig. II.

Diagram of the load transducing platform used in parts 2, 3, and 4 of the experimental programme. Component parts indicated by numbers are: 1. the piezo-electric load cell. 2., a hard plastic sleeve. 3. a 10 inch square by 2 1/2 inch thick cement block. 4. aluminum disc. 5. brass ring. 6. the landing platform bolted solely to the load cell. amount of sliding was very small indeed). The assembly was cast in concrete, with the addition of a brass ring to transfer force to a solid floor and to allow removal of the bottom bolt. An aluminum-and-plywood landing platform on top completed the apparatus. The concrete served as a rigid, non-resonant, support, and also as a heat-sink to protect the temperature-sensitive gauge. No resonance was detectable in the unloaded system below 1000 c.p.s.: there was some highly damped, insignificant, vibration above this frequency. The system produced an output that was linearly related to force applied up to at least 1000 pounds, and from D. C. to 20 kilocycles, with no phase shift.

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The composite recording apparatus used with the first eight subjects in this experiment is shown in Figure 12.

Somewhat different equipment was used with the second set of eight subjects. The e.m.g. was recorded as before. However, it was also fed into a Burns averaging computer (Burns, Ferch, Mandl, 1965), where the e.m.g. was gated, put through a Schmidt trigger, and hence, converted into a pulse form, the frequency of which closely corresponded to the frequency of e.m.g. spikes. In this manner, 100 to 200 steps could be averaged on-line and an immediate readout obtained of e.m.g. frequency versus time after moment of contact with the ground. A microphone beside the point of contact supplied a triggering signal to start a single computer sweep, which lasted 400 msec. (broken up into successive 4 msec. segments for averaging). The computer readout could be conveniently recorded later from an oscilloscope display, using a Polaroid oscilloscope camera. The complete apparatus is diagrammed



Fig. 12.

Composite recording arrangement. 1. Medial side of subject's right leg. 2. e.m.g. electrodes. 3a. Linkage fixing centre shaft of potentiometer to tibia. 3b. Linkage fixing body of potentiometer to sole of foot. 4. Force transducing platform. 5. Charge amplifier. 6. Microphone. 7. Multi-channel oscilloscope.

#### Procedures

The first eight subjects ("Group I" subjects) were instructed to step downwards onto the force-transducing platform, so as to land on it with the ball of their feet. (The right leg was used for e.m.g. recording, and the subjects always landed first on this foot.) They were also to continue smoothly onto their other foot, performing a two-step manoeuvre as naturally as possible. It was found that the e.m.g. activity associated with the first step was completed long before the subject shifted his weight onto his second foot, thus allowing the first step to be examined independently of the second. The steps were from 5, 10, and 15 inch heights, and each was repeated several times.

The second eight subjects ("Group II" subjects) stepped down from similar 5, 10, and 15 inch heights, the sole differences being that they landed on the floor, not on the force-transducing platform, and they were instructed to step outwards and down, so as to avoid the problem of subjects merely letting themselves down, rather than stepping down, from the 5-inch platform. They also performed 100 to 200 identical steps rather than the limited number of the first eight subjects.

#### Data Analysis

The recordings obtained from Group I subjects using the Shackman camera were projected and traced on paper in enlarged form. All jumps of one



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Fig. 13. C

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Composite diagram of the equipment used to determine the average e.m.g. response to landing from a step by means of the Burns Computer. Subjects stepped down 5, IO, or 15 inches to determine an average response at each height. The e.m.g. response was gated, converted into pulses, and averaged, starting at the moment of contact with the ground in each case. This time was determined by means of a microphone near the point of landing. The computer-averaged response was simultaneously displayed on the oscilloscope, and recorded on Polaroid film. height for one subject were superimposed (with reference to the moment of contact with the ground) to try and detect significant patterns of e.m.g. activity. The following were also measured on each record for each subject: time from contact with ground to maximum force exertion, the magnitude of the maximum force, time from contact to maximum rate of change of force, magnitude of the maximum rate of change of force, time from start of e.m.g. activity to moment of contact, time from moment of contact to end of e.m.g. activity, and time from contact to the moment of maximum e.m.g. activity. The last three values were also recorded for soleus. Average values, S. D.'s and S. E. 's of each measurement were obtained for each subject at each height, and overall averages, S. D. 's and S. E.'s for all subjects at the three heights were calculated for all seven measurements. In all cases, for easier comparison of data, forces exerted by the subject are expressed as multiples of his own weight (designated "W"). Hence a force of 1.5W is 1.5 times the static weight of the subject.

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The following values were obtained for the 15 inch step from the one subject whose ankle angle was measured: time from start of ankle extension to contact, time from contact to start of flexion of the ankle, time from contact to maximum flexion, the angle at maximum flexion, the time from contact to the maximum rate of change of ankle angle, and the maximum rate of change of ankle angle. Average values, S. D.'s, and S. E.'s were calculated.

The Polaroid recordings obtained from Group II subjects could only be used to measure an average time from contact with the ground until the end of the landing burst of e.m.g. activity. This was done for each subject,
and an overall average, S. D., and S. E. of these mean values determined for all subjects. For purposes of comparison, averages, S. D.'s, and S. E.'s of the mean values for subjects in Group I were also calculated at this point.

61

The time from contact until the end of the e.m.g. burst was of vital importance in answering Question 2. It was therefore particuarly carefully checked, and the "t" test used to determine if Group I and II subjects differed significantly in this value, or if either differed significantly from the functional stretch reflex time previously determined. The "t" test table derived by Student was used in this and all succeeding tests of significance of difference. One obviously very anomalous subject was discarded from Group I on the basis of this test, on the grounds that his mean response differed widely (p < .001) from that of the others. The significance of the differences between the other six values obtained at different heights of stepping were also examined.

# Part 3:

Is the pattern of neuromuscular activity associated with landing different for (a) a single step to the ground, and (b) repetitive landing, as in hopping at a constant rate, which would permit prediction of the moment of landing on the basis of muscle afferent information?

#### Apparatus

Again, two groups of subjects were used, as in Part 2. Similar recording devices were used, also. (Figures 12 and 13). Instead of stepping from platforms of different heights, however, the subjects hopped rhythmically up and down on one foot on the platform or on the floor. A repetitive, transient sound cue was produced to hold the Group I subjects to a set hopping frequency. This was a gated square wave, originating in a Hewlett-Packard low frequency function generator, and played out through an ordinary speaker.

## Procedure

Group I subjects were instructed first to hop up and down while the frequency of the sound cue was slowly varied between 1 and 3 c.p.s. They would indicate when they felt most comfortable, three times as the frequency was increased, and three times as it was decreased. It was always possible to find their preferred frequency in this fashion within 0.05 c.p.s. They were then instructed to follow the auditory cue and hop up and down on the forcetransducing platform at this frequency, and at 0.4 c.p.s. faster, and 0.4 Recordings were obtained from soleus in four subjects as before.

Group II subjects hopped up and down on the floor 200 times, at whatever frequency they desired, without a cue, which inevitably was their preferred frequency.

#### Data Analysis

In Group I subjects, at each frequency of hopping, the seven parameters of force and e.m.g. activity described in Section 2 were recorded, and averages for each subject calculated. Also, records were superimposed to look for significant patterns as before. The average, S. D., and S. E. of the eight mean values of the seven parameters were calculated. The average preferred frequency, too-fast frequency, and too-slow frequency were also determined. The averages of the eight mean values were examined to see if they changed significantly with speed of hopping.

A computer average of the time from moment of contact with the ground until the end of the e.m.g. burst was determined for each Group II subject. An average, S. D., and S. E. of these mean values was calculated. The average of the Group I means was then compared to the average of the Group II means to see if they differed significantly.

#### Part 4:

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What would the pattern of neuromuscular activity be if the moment of landing were totally unpredictable, such as in a sudden fall at an unpredictable moment?

## **Apparatus and Procedure**

Eight subjects took part in this experiment. A strong electromagnet was suspended by means of a block and tackle and the subject grasped a metal handle attached to it (Figure 14). He was then hoisted off the ground so that his toes were from 1 to 8 inches above the force-transducing platform (Figure 11). After measuring this distance, the experimenter could then shut off the current to the magnet at an unpredictable moment, and a perfectly quite, unheralded, and unimpeded drop was obtained. The gastrocnemius e.m.g., moment of contact with the platform, and force were recorded as before. The moment of release was marked by the breaking of a small electric current, passing from the magnet to the handle. All results were recorded on film using the Shackman oscilloscope camera.

#### Data Analysis

The film record obtained was projected and hence enlarged for analysis. In each drop, the time from the start of the fall until e.m.g. activity started, the time taken to reach the ground, and the maximum force exerted by the ball of the foot were determined. Average values for all three parameters were determined at each height of fall, and the average time from start of fall



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# Fig. 14.

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Electromagnetic device used to drop subjects at non-predictable moments. The subject grasped the handle, which was attracted to the electromagnet when the latter was activated by a suitable power source. The magnet and subject were raised by means of a block and tackle, and the distance from the subject's toes to the landing platform was measured. Sudden, silent release of the subject occurred when the power to the magnet was shut off. 66

to start of e.m.g. activity was calculated for each subject. An overall average, S. D., and S. E. was also obtained (all subjects, all falls.).

The time taken for this "dropping reflex", the functional stretch reflex time found in Part I, and the time taken for a voluntary response to an auditory cue were all compared to see if any significant difference was present between any pair of these values.

## Part 5:

67

Is the activity in a muscle contracting in an isometric fashion altered by subjecting a subject to rhythmic vertical accelerations?

## **Apparatus**

Ten subjects were used in these experiments. Each was placed in a special aluminum-plywood-canvas frame so that he was lying horizontally, but his head was essentially vertical. By means of a cable going to parallel springs, the entire frame and subject, or one end of the frame (the other end being fixed), could be made to rhythmically oscillate (Figure 15). Oscillation was performed by hand, and since the springs, and mass of the subject, set a natural frequency, it, and the amplitude of oscillation, were easy to hold constant. The subject's legs were cradled in foam rubber to prevent their moving. The gastrocnemius – soleus e.m.g. was recorded, as before, and an accelerometer mounted on the apparatus was used to give an indication of accelerations applied to the subject. A time base was also monitored. The e.m.g. was fed through a mean frequency meter that gated it and sent out a signal that was proportional to the frequency of spikes sampled at 16 msec. intervals. Thus a continuous histogram of e.m.g. spike frequency versus time was recorded. All data was permanently recorded by an ultraviolet galvanometer recorder.

## Procedure

Each subject was oscillated in the three manners described above



## Fig. 15.

Diagram of the apparatus used to oscillate subjects while recording the gastrocnemius-soleus e.m.g. activity. The number of springs acting in parallel and the combined weight of the subject and the aluminumcanvas frame determined the frequency of oscillation. The amplitude of oscillation was maintained constant by hand, requiring a very slight force during both upward and downward movement. Accelerations of the frame, the gastrocnemius-soleus e.m.g., and a simultaneous trace representing the averaged frequency of the e.m.g. were displayed on the oscilloscope and recorded on an ultraviolet galvanometer recorder. (whole body, rotating about feet, rotating about head - Figure 15). Each was requested to tense his legs maximally and constantly throughout the experiment. Each went through two minutes of oscillation before going without pause into the experimental run, to allow the subject to become used to the oscillation.

## Data Analysis

69

Twenty to thirty cycles of each type of oscillation were averaged for each subject by adding the histograms together, synchronizing with respect to the moment at which the frame was at the top of its cycle. In this way, a plot of e.m.g. spike frequency versus place in oscillation cycle was obtained. All these plots were then subjected to a three-point averaging process, whereby each point was replaced by the average of it, the point before, and the point after. Using these new curves, plots of the point of maximum activity in a cycle versus frequency of oscillation were obtained, for all three types of oscillation, and all subjects.

Part 1:

Figures 16 to 18 are representative original records of (Figure 16) a monosynaptic response to a tendon tap, (Figure 17) a voluntary muscle contraction following an auditory cue, and (Figure 18) the response when resisting an applied and maintained dorsiflexing force to the foot, all in the same subject.

Similar results were obtained from all subjects. When the cue was a tap to the Achilles' tendon, a monosynaptic discharge was evident in the gastrocnemius e.m.g. 35 to 40 msec. after the tap, and the e.m.g. response corresponding to voluntary activity occurred much later. A summary of the results obtained from all subjects is given in Table 3. This gives the overall average value, overall S. D., and overall S. E.



Fig. 16.

71

The monosynaptic e.m.g. response in the gastrocnemius-soleus muscles resulting from a tap to the achilles' tendon. The sound of the tap is seen followed rapidly by the monosynaptic response in the gastrocnemiussoleus e.m.g., with no response in the dorsiflexor muscle e.m.g. No significant force is generated by the monosynaptic reflex, as seen here.



Fig. 17. The e.m.g. activity in the gastrocnemius-soleus group of muscles during a voluntary ankle extension occurring as rapidly as possible after an auditory cue. The sound of the click by the subject's ear is seen, followed about 250 msec later by the e.m.g. activity in gastrocnemius-soleus, and then by a force exerted by the ball of the foot. Minimal e.m.g. activity was present in the ankle dorsiflexor muscles at the time of the auditory cue in this particular case, and more activity followed that in the extensor muscles.





The e.m.g. activity in the gastrocnemius-soleus group of muscles during as rapid as possible opposition to an applied and maintained dorsiflexing force to the foot. The moment of application of the force is noted as a sudden upwards displacement of the force tracing. This is followed about 100 msec later by the gastrocnemius-soleus e.m.g. response. E.m.g. activity was present in the ankle dorsiflexing muscles to a small degree throughout in this case.



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Fig. 16. The monosynaptic e.m.g. response in the gastrocnemius-soleus muscles resulting from a tap to the achilles' tendon. The sound of the tap is seen followed rapidly by the monosynaptic response in the gastrocnemius-soleus e.m.g., with no response in the dorsiflexor muscle e.m.g. No significant force is generated by the monosynaptic reflex, as seen here.



Fig. 17. The e.m.g. activity in the gastrocnemius-soleus group of muscles during a voluntary ankle extension occurring as rapidly as possible after an auditory cue. The sound of the click by the subject's ear is seen, followed about 250 msec later by the e.m.g. activity in gastrocnemius-soleus, and then by a force exerted by the ball of the foot. Minimal e.m.g. activity was present in the ankle dorsiflexor muscles at the time of the auditory cue in this particular case, and more activity followed that in the extensor muscles.



Fig. 18. The e.m.g. activity in the gastrocnemius-soleus group of muscles during as rapid as possible opposition to an applied and maintained dorsiflexing force to the foot. The moment of application of the force is noted as a sudden upwards displacement of the force tracing. This is followed about 100 msec later by the gastrocnemius-soleus e.m.g. response. E.m.g. activity was present in the ankle dorsiflexing muscles to a small degree throughout in this case.



# Table 3.

Summary of results obtained in part 1 of the experimental program. Eight specific measurements taken of records obtained are described. The average value in msec. for each, the S.E. of that average, and the number of values recorded to determine each average are given.

a

	N Laimber of		
	insec.	observ.j	S.E
Time from auditory cue to voluntary e.m.g. response (msec.)	E 9 1	85	8.1
Time from tap to side of foot to voluntary e.m.g. response (msec)	<i>। 5</i> १	57	د.6
Time from tap to Achilles' tendon to voluntary e.m.g. response (msec.)	163	73	6.8
Time from tap to Achilles' tendon to voluntary e.m.g. response (msec.) (gastrocsoleus under initial tension)	148	75	4.5
Time from applying and maintaining a dorsiflexing force to the foot to emig. response (msec)	119.5	34	3.5
Latency between 1st electrical and 1st. mechanical muscle events (random vol. twitch? (nsec.)	<b>27</b> .7	85	0.8
Latency of monosynaptic reflex (msec) (tap Achilles' tendon)	37	74	0.5
Latency of monosynaptic reflex (msec) (tap ball of foot)	36	13	0.95

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 $\left( \begin{array}{c} \\ \end{array} \right)$ 

Table 3.Summary of results obtained in part 1 of the experimental program.Eight specific measurements taken of records obtained are described.The average value in msec. for each, the S.E. of thataverage, and the number of values recorded to determine eachaverage are given.

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Figure 19 is a typical response to a 12-inch step onto the forcetransducing platform. The recording of force exerted by the ball of the foot starts with a small transient rise, which falls off to nearly zero at 5 msec., before commencing a smooth rise, interrupted from 15 to 20 msec. by another transient force. The first hump is apparently due to the subject's toes hitting the platform first and bending upwards until the ball of the foot strikes. The cause of the second is not certain, but is probably due to a mechanical phenomenon, since it occurs much too early for a reflex one. The force rises smoothly and rapidly from 20 msec. after initial contact, peaking at about 110 msec. and stabilizing at 1W (subject standing on the platform) by about 450 msec. Again, "W" designates the static weight of the particular subject. The maximum force reached was only 1.9W. E.m.g. activity in the gastrocnemius – soleus group started about 140 msec. before contact and is essentially over at 120 msec. after contact. Following this is e.m.g. activity related to a balancing effort of the subject, who in this case remained standing on one leg on the force-transducing platform.

Not all records were as clear as that of Figure 19, so an attempt was made to superimpose three or four records of a subject performing the same manoeuvre, to see if any clearer pattern emerged. The individual e.m.g. tracing was started at the first discernible spike of activity in each case, and all were synchronized with respect to the moment of landing. Figure 20 is an example of the result, and it clearly demonstrates the e.m.g. burst as shown in the single record of Figure 19. It was possible, using both single and superimposed





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Fig. 19. E.m.g. activity in gastrocnemius-soleus muscles associated with landing from a jump to the ground. This record of a 12 inch jump shows the typical smooth buildup and subsequent fall-off to 1 "W" of the force exerted by the ball of the foot. The e.m.g. activity is seen to take the form of a spindle-shaped burst, centered just before the moment of landing, which is indicated by a sudden upwards deflection of the force tracing. A period of decreased activity follows this burst. The second burst noted is due to the subject stepping off the force-transducing platform.





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Fig. 20. E.m.g. activity in gastrocnemius-soleus muscles associated with landing from a jump to the ground. All records from one subject. Each record has three consecutive traces superimposed, synchronized with respect to the instant of landing. The dot at the start of each trace marks the first detectable e.m.g. activity associated with that landing. recordings from eight subjects, to measure the seven parameters listed under "Methods" for each. Overall averages, S. D.'s, and S. E.'s were calculated.

76

A second set of stepping experiments was performed on eight new subjects using the Burns computer to average the e.m.g. spike frequency as described. The readout of the computer was displayed on the oscilloscope face and recorded, and an original record is shown in Figure 21.

Since the moment of landing was used to trigger the computer sweep, no e.m.g. is shown at about 130 msec. after landing. This sudden end was characteristic, though not always as obvious as in this record. The cut-off was usually followed by a short (20 - 40 msec.) period of limited e.m.g. activity, which in turn was replaced by an increased level of activity, sometimes including a hump of higher spike frequency before becoming constant, as shown in Figure 21. Much of the activity after the relatively silent period at 130 - 150 msec. was probably due to a balancing effort on the part of the subject, as he shifted onto his other foot. It should be noted that the hump of e.m.g. activity at about 60 msec. after landing shown in this record is not typical of the responses obtained from other subjects.

As mentioned previously, the most important measurement in this part of the project is the time from moment of contact with the ground until the e.m.g. burst (of landing) is over. It was evident, by comparing individual results of Group I subjects, that one subject (R. P.) was behaving very differently from the others, probably because he was gradually letting himself down by means of the "non-landing" leg, rather than stepping immediately onto his second foot



## Fig. 21.

Readout of the computer average of the gastrocnemius-soleus e.m.g. spike frequency during 150 consecutive 10 inch steps. Starting at the moment of landing, the following 400 msec. is broken up into 100 4 msec long segments. The deflection of the dot in each segment of time is proportional to the total number of e.m.g. spikes occurring during that particular segment in all 150 steps. The e.m.g. activity associated with landing is seen to nearly cease at about 135 msec. after landing, but to build up again at about 175 msec.



Fig. 21. Readout of the computer average of the gastrocnemius-soleus e.m.g. spike frequency during 150 consecutive 10 inch steps. Starting at the moment of landing, the following 400 msec. is broken up into 100 4 msec long segments. The deflection of the dot in each segment of time is proportional to the total number of e.m.g. spikes occurring during that particular segment in all 150 steps. The e.m.g. activity associated with landing is seen to nearly cease at about 135 msec. after landing, but to build up again at about 175 msec. as requested. Specifically, his time from contact until eng of e.m.g. burst was much greater than that for the others: indeed, it was apparently indefinitely prolonged on occasion. For instance, the following graphs (Figures 22, 23) are plots of this time against height of step. Figure 22 compares subject R. P. against overall values for Group I subjects, excluding him. He is more than two standard deviations removed from the overall average values. Figure 23 illustrates the difference in overall Group I results if R. P. is removed, in this case using overall mean values, S. D.'s, and S. E.'s.

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Figure 24 compares Group I (excluding R. P.) and Group II subjects with regard to the time between contact with the ground and the end of the major e.m.g. burst. Shown are plots of this value against height of step for each group, the overall average (for all heights) for each group, and a grand overall average (all groups, all heights). Also indicated is the time before which the functional stretch reflex could not occur, on the basis of findings of this experimental study (i.e., 15 msec. after contact before ankle flexion commences, and 119.5 msec. for the functional stretch reflex). It should be repeated that all averages, S. D.'s, and S. E.'s are those of the mean values for each subject (i.e., in the case of Group I (excluding R.P.), the average is that of the seven mean values obtained from the subjects). Letters are used in Figure 24 to indicate each of the eight specific values plotted. Table 4 is the statistical comparison of these eight points. It shows the "P" value (probability that the difference between the two points is due to chance) for each pair. Note that there is no significant difference between any of these values (all "P"'s above the .05 level). This confirms that the two methods by



Fig. 22.

Graphs of time from moment of landing until the end of the gastrocnemius-soleus e.m.g. burst associated with landing versus the height of the step. Subject R.P., the only markedly anomalous one, is compared to all other group I subjects, excluding him. Overall averages, standard deviations, and standard errors are given at each point on the graphs.



Fig. 23.

Graphs of time from moment of landing until the end of the gastrocnemius-soleus e.m.g. burst associated with landing versus the height of the step. All group I subjects, and group I subjects excluding R.P., are compared. Overall averages and standard errors are given for each point on the graphs. Also shown are the overall averages (all heights) for the two groups.



# Fig. 24.

Graphs of time from moment of landing until the end of the gastrocnemius-soleus e.m.g. burst associated with landing versus the height of the step. Group I subjects excluding R.P. are compared to Group II subjects. The overall averages for both groups with all heights combined, and for all groups, all heights, are also shown. Standard errors are given for each point. The time before which the functional stretch reflex cannot produce any e.m.g. response is also indicated by a dashed line.





12

A statistical comparison of the points plotted on the graph of Fig. 24. Each point is identified by a letter, and the pairs of points compared are listed along with the "P" value of their difference. (The "P" value is the probability that the difference between the point is due to chance alone). Since there is no significant difference between any pair of points, it may be concluded that the time from contact with the ground to the end of the gastrocnemius-soleus e.m.g. burst during a step is independent of the height of the step.

Compare	<u>`P`</u>
A - G	>.05
B - C	>.10
A - C	>.50
D-E	>.70
E - F	>.20
D-F	>.(0
A - D	>.10
B-E	> .70
C - F	>.20
G-H	2.10

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Table 4. A statistical comparison of the points plotted on the graph of Fig. 24. Each point is identified by a letter, and the pairs of points compared are listed along with the "P" value of their difference. (The "P" value is the probability that the difference between the point is due to chance alone). Since there is no significant difference between any pair of points, it may be concluded that the time from contact with the ground to the end of the gastrocnemius-soleus e.m.g. burst during a step is independent of the height of the step. which the two groups of subjects were handled gave equivalent results, and that height of step did not significantly affect the time between contact with the ground and the end of the e.m.g. burst.

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The functional stretch reflex time as determined in Part 1 was also compared with the overall mean of Group I subjects (excluding R. P.) (all heights included), the overall mean of Group II subjects (all heights included), and a grand overall mean of all subjects and heights of Group I (excluding R. P.) and Group II. The Group II value was shown to be significantly less than the functional stretch reflex time, while the other two values were not significantly different from it.

Due to the fact that subject R. P. was excluded from the Group I data, the values for the other six parameters measured had to be recalculated. Table 5 is a summary of this data. Figures 25 to 30 are graphs plotting the new values against height of step. All parameters were examined to detect significant differences in values depending on height of step. If two points are significantly different, they are joined on the graph by a solid line. If the two points do not differ significantly, they are joined by a broken line.

It was indicated under "Methods" that recordings from soleus were obtained from four subjects doing 15-inch steps. The data obtained is summarized in Table 6.

Also, in one subject, the angle formed by the ankle was continuously followed. An example of an original record is given in Figure 31.

The average values for that subject are given in Table 7.









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 Table 5.
 Summary of the results obtained from group | subjects (excluding R.P.) during experiments involving landing from a step to the ground. Overall averages, standard deviations, and standard errors are shown for each of the quantities calculated, at stepping heights of 5, 10, and 15 inches. The number of observations used to calculate the overall averages is shown in brackets after each S.D. The values obtained for the same quantity at different heights of stepping are compared at the bottom of the table.

		о с I	(	dF	e.m.g. start	confect	contact-a
	Lontact -	lox F	Contect ->	max dt	- contact	eng end	max e.m g. act
	max F (nsec.)	(w »)	max at (msec)	(W7sec)	(msec.)	(niec)	(ASOC)
15" STEP	1						
overall average	115	2.2	47	37	152	131	-10.2
5.D.	29.1 (16)	.56 (16)	17.9 (10)	20.6 (16)	58.9 (16)	62 (16)	25.8 (16)
•• S. E.	7.3	. 14	4.5	5.2	14.7	15.5	6.5
10" STEP							
overall average	166	1.8	64	23	161	115	3.6
	64.3 (16)	. 61 (16)	22.2 (16)	16.2 (16)	61 (16)	37 (16)	23.6 (16)
·· \$.E.	16.1	.15	5.6	4.1	15.3	9.3	5.9
5" STEP							
overall average	214	1.4	92	17	113	148	5.12
	73 (17)	.39 (17)	34.4 (17)	15.1 (1	50.8 (17)	55 (15)	32.7 (15)
s.ê.	7.7	. 09	8.3	3.7	12.3	14.2	8.4
P values (5- 10	.05 + 10	· <u>02 - + .05</u>	.00101	. 20 30	. <u>01 -&gt; .02</u>	.1020	· <u>01 -&gt; .01</u>
for (5-15	5.001	4.001	6.001	.00101	.0205	.50 60	5.001
omparisons (10-15 signif dift.)	.001-+.01	.05 -+ .10	.02 > . 125	.02-+.05	.50 -> .60	.0510	.10 -> .20
( underlined /							

# Summary of Stepping Results Group & review , subject +++

Table 5. Summary of the results obtained from group I subjects (excluding R.P.) during experiments involving landing from a step to the ground. Overall averages, standard deviations, and standard errors are shown for each of the quantities calculated, at stepping heights of 5, 10, and 15 inches. The number of observations used to calculate the overall averages is shown in brackets after each S.D. The values obtained for the same quantity at different heights of stepping are compared at the bottom of the table.







Fig. 26.

Fig. 25.

Graph plotting time from the moment of contact with the ground in landing from a step until the maximum rate of change of force is experienced by the foot versus the height of the step. The overall average and standard error are plotted for each point.



Fig. 27. Graph plofting the maximum force experienced by the ball of the foot while landing from a step versus the height of the step. The overall average and standard error are plotted for each point.



Fig. 28. Graph plotting the maximum rate of change of force experienced by the ball of the foot while landing from a step versus the height of the step. The overall average and standard error are plotted for each point.









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Fig. 30. Graph plotting the time interval between contact with the ground and maximum gastrocnemius-soleus e.m.g. activity when landing from a step to the ground versus the height of the step. The overall average and standard error are plotted for each point.



Fig. 31.

Measurement of the angle formed by the ankle during the landing from a 15 inch step to the ground. The moment of landing is indicated both by the spike of sound on the microphone tracing, and by the sudden upwards displacement of the force tracing, which then follows a normal course for a step to the ground. It may be seen that the ankle starts to extend hundreds of milliseconds before contact with the ground, starts to suddenly flex about 15 msec after this point, and is maximally flexed just after 200 msec after contact with the ground. It can also be seen that this maximal angle of flexion is roughly that maintained by the ankle while standing normally.

15 inch Steps (Soleus)	e.m.g. start -= contact (msec.)	contact-+ e.m.g. end (msec.)	contact max. e.m.g. activity (msec.)
overall average	19	139	98
S.D.	17.7 (7)	12.1 (5)	22.8 (7)
<b>S.E</b> .	6:8	5.9	8.7

Table 6. Summary of the e.m.g. response of soleus when landing from a 15 inch step to the ground. The overall average value, the standard deviation, the standard error, and the number of observations (in brackets) are all given for each of the quantities measured.



Fig. 31. Measurement of the angle formed by the ankle during the landing from a 15 inch step to the ground. The moment of landing is indicated both by the spike of sound on the microphone tracing, and by the sudden upwards displacement of the force tracing, which then follows a normal course for a step to the ground. It may be seen that the ankle starts to extend hundreds of milliseconds before contact with the ground, starts to suddenly flex about 15 msec after this point, and is maximally flexed just after 200 msec after contact with the ground. It can also be seen that this maximal angle of flexion is roughly that maintained by the ankle while standing normally.

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	value	S.D.	S.E.
start of ankin exterior	397	74 (13)	1 <b>7:6</b> %
context start of flame	(// 6	6.6 (j)	F.6
caltact - Auginty - fillenst	238	20.5 (1)	
	78	2.7 . (2.0)	0.6
content - Repairing total of change at all and a (near)	44	(•)	7.6
maximum ruja at salaga at ankle ungle (?/sec.)		76 (19)	21 <b>8</b>

Summary of the results of measurements of the angle formed by the ankle while landing from a 15 inch step to the ground. The overall average value, the standard deviation, the standard error, and the number of observations (in brackets) are all given for each of the quantities measured.

Subject"	Fast	Natural Frequency	Slow
71	2.45/14c.	2.05/sec.	1.65 / sec.
2 3	2.45	2.05	1.65
•	1.50	1.10	1.70
5	· · · · · · · · · · · · · · · · · · ·	1.05 -	
7	3.60	1.10	1.30 -
8	<u></u>	2.05	

Table 8.

Table 7.

Summary of the rate at which the 8 subjects in group 1 hopped during part 3 of this experimental programme. Their natural frequency was first determined, and then most were driven by an auditory cue at that frequency, and 0.4 cps faster and slower. Average natural, too fast, and too slow frequencies were calculated.

#### Part 3:

90

This part of the project was done with the same two groups of subjects as Part 2. However, subject R. P. was included as he gave similar results to the other subjects in this section.

Prior to performing any experiments with the Group I subjects, their natural frequency of hopping was determined as described. This, and a faster, and slower, frequency were used in the hopping experiments, as detailed in Table 8. The average frequency at each speed was used later to plot the seven parameters (as in Part 2) against hopping rate.

Figure 32 illustrates a typical original result from a hopping experiment.

As in Part 2, several records were superimposed for each frequency with each subject to look for patterns of e.m.g. activity that might emerge. Tracings were started with the first spike of activity of the hop, and cut off with the last spike. No e.m.g. activity at all was present before or after. An original result is shown in Figure 33.

The pattern is certainly different from that seen in the case of a single step. The force buildup is smoother and slower, and more symmetrical, as the subject launches himself into the next hop. Peak force is again surprisingly small (2.1 "W" versus 2.2 "W" in a 15-inch step), and is reached about 160 msec. after initial contact with the force-transducing platform (compared to 110 msec. in the case of a 15-inch step). The e.m.g. activity starts about 100 msec. before contact with the platform (Figure 33), but is prolonged until about 260 msec. after contact, as a sustained burst. There is a suggestion of

load extensor EMG<flexor sound 100 cps

91

# HOPPING AT PREFERRED FREQUENCY (2.15 cps)

Fig. 32.

The e.m.g. response of the gastrocnemius-soleus group of musc, les to repetitive hopping at the subject's preferred frequency. The moment of contact with the ground when landing from a single hop is shown by a blip in the microphone tracing. The force exerted by the ball of the foot is of low magnitude and smoothly increases and decreases. The gastrocnemius-soleus e.m.g. starts well before contact with the ground, and is prolonged to over 250 msec. after contact. It starts again 50 to 70 msec after leaving the ground on each hop. The flexor muscle e.m.g. tends to be active when the gastrocnemius-soleus group is not in this case.



Fig. 33.

E.m.g. activity in gastrocnemius-soleus muscles associated with landing from one of a series of repetitive hops at the subject's preferred frequency. Five consecutive traces are superimposed, synchronized with respect to the instant of landing. The dot at the start of each individual trace marks the first detectable e.m.g. activity associated with landing from that hop.



# HOPPING AT PREFERRED FREQUENCY (2.15 cps)

Fig. 32. The e.m.g. response of the gastrocnemius-soleus group of musc les to repetitive hopping at the subject's preferred frequency. The moment of contact with the ground when landing from a single hop is shown by a blip in the microphone tracing. The force exerted by the ball of the foot is of low magnitude and smoothly increases and decreases. The gastrocnemius-soleus e.m.g. starts well before contact with the ground, and is prolonged to over 250 msec. after contact. It starts again 50 to 70 msec after leaving the ground on each hop. The flexor muscle e.m.g. tends to be active when the gastrocnemius-soleus group is not in this case.



Fig. 33. E.m.g. activity in gastrocnemius-soleus muscles associated with landing from one of a series of repetitive hops at the subject's preferred frequency. Five consecutive traces are superimposed, synchronized with respect to the instant of landing. The dot at the start of each individual trace marks the first detectable e.m.g. activity associated with landing from that hop.

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a large, synchronous spike at about 50 msec. in this and somewhat more than half of the other records obtained. This could correspond to the monosynaptic response (36 msec., plus about 15 msec. after contact before the ankle angle starts to change).

92

The results obtained from all subjects of Group I are summarized in Table 9.

As in Part 2, a more accurate estimate of the time from contact until the e.m.g. burst was obtained with a second group of subjects and a computerized averaging system. An original record obtained is shown in Figure 34.

The average of mean values obtained with Group II subjects (266 msec., S. D. 25, S. E. 8.8) was compared to that derived from the Group I results, and the two values were shown not to differ significantly from one another (.8 "P" .9). Averages, S. D.'s, and S. E.'s of the eight mean values for each item were used.

Averages (of mean values) for slow, normal, and fast frequencies of hopping for each parameter measured were also examined to detect significant differences due to rate of hopping. This is indicated on the graphs of Figures 35 to 40, which plot the various parameters against frequency of hopping. On each graph, as in Part 2, if two points are joined by a solid line, they are significantly different, but if joined by a dashed line, they are not significantly different.

Again, in four subjects, results were obtained from soleus only. These are summarized in Table 10.



Table 9.

Summary of the results obtained from group I subjects during experiments involving hopping at several frequencies. The average of the subject means, and the standard deviation and standard error of this value are shown for each of the quantities calculated, at the preferred hopping frequency, and at a too-fast and too-slow frequency. The number of means used to calculate the averages is shown in brackets after each S.D.

	[Group I]						
	Contact-> max.F.(nsec)	Max. F. "W"s	Contact-+ max. <u>dF</u> (msec)	max. <del>dF</del> dt W/scc	e.m.g.start -scontact (msec.)	contact -> e.m.g. end (msec.)	synch. «.m.g. burst (msec.)
nat. frequency							
av. of means	161.9	2.0	76.6	19-1	84.1	262.7	47.4
S.D	20.1 (8)	.55 (8)	15.2 (8)	4.5 (8)	27.3 (8)	26.3 (7)	10.1 (J)
<u>Sé</u>	7.1	.19	5.4	1.6	9.6	10.0	4.5
fast							
as of means	136.5	2.1	65.0	24.7	68.0	190.8	37.5
S.D	20.9 (6)	.35 (4)	12.5 (6)	6.8 (6)	16.3 (6)	23.9 (5)	3.5 (2)
S.E	· 8.5	. 14	5.1	2.8	6.7	10.7	2.5
slaw							
av, of means	219.8	1.7	89.3	(3-8	107.3	360.5	49.3
<u>sp</u>	37.5 (6)	.25 (6)	27.0 (6)	4.2 (6)	24.7 (6)	21.2 (4)	16.1 (3)
S.E	15.3	.10	11.0	1.7	10.1	10.6	9.3

Summary	of	Ho	pping	_ h	esults
)	Ger		T)		

### Table 9.

Summary of the results obtained from group I subjects during experiments involving hopping at several frequencies. The average of the subject means, and the standard deviation and standard error of this value are shown for each of the quantities calculated, at the preferred hopping frequency, and at a too-fast and too-slow frequency. The number of means used to calculate the averages is shown in brackets after each S.D.

# Readout of the computer average of the gastrochemius-soleus

94

e.m.g. spike frequency during 200 consecutive hops at the subject's preferred frequency. Starting at the moment of landing, the following 400 msec . is broken up into 100 4 msec . long segments . The deflection of the dot in each segment of time is proportional to the total number of e.m.g. spikes occurring during that particular segment in all 200 hops. The e.m.g. activity associated with landing from a hop is seen to be sustained at a nearly constantlevel until 220 msec. after initial contact with the ground, and to end at about 280 msec.

пор (	Soleus)	9: e.m.g. 	tact	e.m.).en. (msec.)	
aver S.D			+ s (.:5)	336 37.4 (	10)
		, <b>, , , , , , , , , , , , , , , , , , </b>			

Fig. 34

Table 10. Summary of the e.m.g. response of soleus when landing from a hop at the subject's preferred frequency. The average, standard deviation, and standard error, as well as the number of observations (in brackets), are all given for each quantity measured.



Fig. 34. Readout of the computer average of the gastrocnemius-soleus e.m.g. spike frequency during 200 consecutive hops at the subject's preferred frequency. Starting at the moment of landing, the following 400 msec. is broken up into 100 4 msec. long segments. The deflection of the dot in each segment of time is proportional to the total number of e.m.g. spikes occurring during that particular segment in all 200 hops. The e.m.g. activity associated with landing from a hop is seen to be sustained at a nearly constant level until 220 msec. after initial contact with the ground, and to end at about 280 msec.

Hops, natifreq (Soleus)	e.m.g. start -> contact (msec.)	contact -> e.m.g. end (msec.)
averaze	34	336
S.D	8.5 (15)	37.4 (10)
S.E	2.2	11.9

Table 10. Summary of the e.m.g. response of soleus when landing from a hop at the subject's preferred frequency. The average, standard deviation, and standard error, as well as the number of observations (in brackets), are all given for each quantity measured.



Graph plotting time from the moment of contact with the ground in landing from a hop until the maximum rate of change of force is experienced by the foot versus the rate of hopping. The average of subject means and standard error are plotted for each point. Eight subjects took part in this section of the project. Each was dropped four to six times from heights that varies from 1 to 8 inches. Figure 41 is an example of the original results recorded in two falls, one of 8 inches, and the other 2.3 inches.

The first arrow in each case indicates the moment of release from the electromagnet, and the second indicates the moment of contact with the force-transducing platform.

The force exerted by the ball of the foot is actually greater in the case of the fall from a lesser height. Also, the buildup of force is more irregular, and rapid, in the latter case. The higher fall produced a smoother, more prolonged, buildup of force applied to the foot. A striking feature of these experiments was that falls from less than about 5 inches were always associated with an uncomfortable jolt on landing, whereas falls from higher levels were not.

Again, if the two falls are compared, it can be seen that the e.m.g. began in both cases about 75 msec. after the start of the fall. This time (75 msec., S. E. 1.4) is considerably shorter than the functional stretch reflex time (119.5 msec., S. E. 3.5), and is much less than the time taken to voluntarily respond to an auditory cue (195 msec., S. E. 8.1). (These three numbers are significantly different from each other, with "P" < .001 in all cases.) It is independent of the height of fall up to falls of at least 1 foot. The pooled results of all subjects are shown in Figure 42, which plots the time, from the start of fall to the beginning of e.m.g. activity, against height



# Fig. 41.

The effect of height on landing from a fall. Illustrated are two original records obtained when the same subject fell 8 and 2.3 inches. In both cases, the gastrocnemius-soleus e.m.g. activity begins about 180 msec. after the start of the fall, and the dorsiflexor muscle e.m.g. starts soon afterwards. Force buildup is smoother and slower in the case of the higher fall, however. Also shown in the manner in which the subject was suspended by his arms from the electromagnet before being dropped onto the force-transducing platform. The prolonged noise shown in the 8 inch fall was due to the moving of cables during the fall. Moment: of contact was determined from the force tracing.



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Fig. 41 The effect of height on landing from a fall. Illustrated are two original records obtained when the same subject fell 8 and 2.3 inches. In both cases, the gastrocnemius-soleus e.m.g. activity begins about 180 msec. after the start of the fall, and the dorsiflexor muscle e.m.g. starts soon afterwards. Force buildup is smoother and slower in the case of the higher fall, however. Also shown in the manner in which the subject was suspended by his arms from the electromagnet before being dropped onto the force-transducing platform. The prolonged noise shown in the 8 inch fall was due to the moving of cables during the fall. Moment of contact was determined from the force tracing.



Fig. 42.

Graph plotting the interval between the start of a fall until the start of gastrocnemius-soleus e.m.g. activity versus the height of fall. All falls for all subjects are included. The overall average of this interval, the standard deviation of it, and the standard error, are also shown. Note that the interval appears to be independent of the height of fall.





Fig. 42. Graph plotting the interval between the start of a fall until the start of gastrocnemius-soleus e.m.g. activity versus the height of fall. All falls for all subjects are included. The overall average of this interval, the standard deviation of it, and the standard error, are also shown. Note that the interval appears to be independent of the height of fall.

of fall.

101

Figure 43 is a summary of data obtained in the dropping experiments. The points plotted represent average values obtained from several subjects for each height. Again, the time from start of fall to start of e.m.g. activity is independent of height of fall, and is about 75 msec. The time falling is also plotted against height of fall, though this could be calculated using simple physical principles. Of interest is the plot of maximum force exerted by the foot versus height of fall, which rises, falls, and goes on rising. It can be seen that falls of 1.5 and 6.5 inches produced nearly the same force. Falls of 4 inches produced a greater transient force than those of 5 to 7 inches.



Fig. 43.

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Graph summarizing the results obtained during experiments involving sudden falls. Curve A plots the maximum force sustained by the bail of the foot versus the height of the fall. It builds slowly to peak at 4 inches, falls off to 6 inches, then rises again. Curve B plots the time taken to reach the ground as measured from the records versus the height of the fall. It rises in the expected manner. Curve C plots the interval from the start of the fall until the first e.m.g. activity in the gastrocnemius-soleus muscles. It is slightly over 70 msec., and is independent of the height of the fall.



Fig. 43. Graph summarizing the results obtained during experiments involving sudden falls. Curve A plots the maximum force sustained by the ball of the foot versus the height of the fall. It builds slowly to peak at 4 inches, falls off to 6 inches, then rises again. Curve B plots the time taken to reach the ground as measured from the records versus the height of the fall. It rises in the expected manner. Curve C plots the interval from the start of the fall until the first e.m.g. activity in the gastrocnemius-soleus muscles. It is slightly over 70 msec., and is independent of the height of the fall.

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Part 5:

103

Ten subjects took part in the oscillation experiments. Figure 44 is an example of the raw results obtained from one of them, while he was being oscillated with his body always parallel to the floor.

Figure 45 shows the collected results for one subject, for which he underwent whole body oscillation, oscillation rotating about his feet, and oscillation rotating about his head. A distinct modulation of the e.m.g. spike frequency is evident; however, a nearly identical one shows up in all three types of oscillation (Note: these are three-point-averaged curves.). Other subjects showed similar modulation of the e.m.g. spike frequency; however, depending on the subject, the degree of modulation could be greatest in any of the three modes of oscillation, with no particular pattern evident.

Figure 46 plots the point of maximum activity in the cycle of oscillation against frequency of oscillation, for all subjects. Since the subjects weighed varying amounts, the frequency with which they oscillated differed, as it did in one subject depending on the type of oscillation. It is readily seen that maximum activity did not occur at any consistent point in the cycle, and that changing the frequency of oscillation, or the mode, also had no apparent effect.



### Fig. 44.

The effect on the gastrocnemius erm.g. spike frequency of vertical linear oscillation of the entire subject. Shown is a continuous record of there mig. resulting from the support moximally tensing his leg, a continuous analysis of the frequency of spikes in the earling, and a face representing accelerations experienced by the subject. Records of this sort were averaged over many continuous cycles to detect variations in the e.m.g. spike frequency dependent upon the pasition in the cycle of oscillation.



Fig. 44. The effect on the gastrocnemius e.m.g. spike frequency of vertical linear oscillation of the entire subject. Shown is a continuous record of the e.m.g. resulting from the subject maximally tensing his leg, a continuous analysis of the frequency of spikes in the e.m.g., and a trace representing accelerations experienced by the subject. Records of this sort were averaged over many continuous cycles to detect variations in the e.m.g. spike frequency dependent upon the position in the cycle of oscillation.



Fig. 45.

Graphs plotting the frequency of gastrocnemius e.m.g. spikes versus the position in the cycle of oscillation during three types of vertical, sinusoidal, oscillation. All results from one subject. Zero degrees indicates the top of the cycle; one complete cycle before and after this point are included. Each curve has been 3point averaged i.e., each point of the original curve has been replaced by the average of the point, the preceeding, and the following one. A modulation of the e.m.g. spike frequency dependent upon position in the cycle of oscillation is apparent in this case. · · ·





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Fig. 45. Graphs plotting the frequency of gastrocnemius e.m.g. spikes versus the position in the cycle of oscillation during three types of vertical, sinusoidal, oscillation. All results from one subject. Zero degrees indicates the top of the cycle; one complete cycle before and after this point are included. Each curve has been 3-point averaged; i.e., each point of the original curve has been replaced by the average of the point, the preceeding, and the following one. A modulation of the e.m.g. spike frequency dependent upon position in the cycle of oscillation is apparent in this case.



Fig. 46.

Graph summarizing the results of experiments involving vertical, sinusoidal oscillation of subjects. The position in the oscillation cycle of maximum gastrocnemius e.m.g. activity is plotted against the frequency of oscillation. Each point represents the position of maximum activity for I subject, determined by averaging all his curves for I mode of oscillation. It is apparent that the position of maximum activity can occur anywhere in the cycle, though perhaps more likely in the 60 to 200 degree range, and that frequency of oscillation has no apparent effect on the position of maximum activity for each type of oscillation.





Fig. 46. Graph summarizing the results of experiments involving vertical, sinusoidal oscillation of subjects. The position in the oscillation cycle of maximum gastrocnemius e.m.g. activity is plotted against the frequency of oscillation. Each point represents the position of maximum activity for I subject, determined by averaging all his curves for I mode of oscillation. It is apparent that the position of maximum activity can occur anywhere in the cycle, though perhaps more likely in the 60 to 200 degree range, and that frequency of oscillation has no apparent effect on the position of maximum activity for each type of oscillation.

## DISCUSSION

The aim of this project was to examine certain aspects of voluntary muscle control in the leg. The stretch reflex has long been thought to play a part in the control of stepping movements in humans, as well as aiding in the control of posture. However, on basic physical principles, it can easily be shown that this reflex is too slow, allowing the person to fall 14 inches more after initial contact with his toes, if he steps down 1 foot. Two alternatives remain: perhaps the stretch reflex is used for fine adjustment of contraction only, after a large burst of uncontrolled tonic activity is fired off (via the direct  $\alpha$ , or the  $\mathcal{X}$  loop route) before landing. Or, the stretch reflex may not function at all during a stepping movement.

The first problem was to demonstrate a functional stretch reflex in the gastrocnemius – soleus group of muscles. Hammond, Merton, and Sutton (1956) have shown that the myotatic reflex in the arm is fastest and most reproducible when caused by a suddenly applied and maintained velocity of stretch to the flexor muscles involved. In the arm, this reflex took from 60 to 80 msec., and though a monosynaptic discharge occurred in the stimulated muscles after only 15 to 20 msec., this had no measurable effect on the force of contraction. The experiments described in this thesis have shown, using gastrocnemius and soleus, that a somewhat similar situation is present in the leg. The delay between stimulus and a voluntary e.m.g. response is minimal, and the values have the least statistical spread, when the input to the muscles is an applied and maintained force. This is in comparison to an input of sudden taps to the Achilles' tendon, light taps to the side of the foot, or a mere auditory cue. It should be noted that even this minimum delay is about 119 msec. (monosynaptic reflex time: 37 smsec.); 28 msec. are also required for the earliest electrical activity of the muscle to be converted into the beginning of the mechanical event of contraction. A minimum delay of 147 msec. is thus required to produce a significant tension in the plantar flexors of the foot in response to dorsiflexion of the ankle.

100

A functional stretch reflex is present in the gastrocnemius – soleus group, having 3.5 to 4 times the latency of the monosynaptic response in the same muscle, and about 65% of the latency of a voluntary response, similar to the case of the biceps in the arm. However, is it functionless in stepping movements, or does it have a fine-adjustment role? For purposes of clarity, Figure 47 is a reconstructed example of the average response to be expected in a 15-inch step.

The solid bar represents the time, following initial contact with the toes, during which the functional stretch reflex cannot function. This is broken up into two sections – 15 msec. before the ankle starts to bend, and 119 msec. for the reflex to activate the muscle. It is immediately obvious that none of the extra burst of e.m.g. activity in gastrocnemius (and essentially none of that in soleus) can be due to a stretch reflex. In the case of a single step, as considered here, it would not be possible for some cerebellar mechanism to phase advance the contraction response, triggered by muscle spindle stretch, as this would take at least the functional stretch reflex time to be initiated.

If control of the leg antigravity muscles was on the basis of a



109





Fig. 47.

109

The predicted response of the gastrocnemius-soleus muscles to a sub-maximal stimulus to their efferent nerve supply. The force that would be exerted by the ball of the foot on the forcetransducing platform is shown. No force would be recorded (though a small amount is probably developing) until 28 msec. after the start of stimulation. Maximal contraction for that level of stimulation is reached in 157 msec.



109

Fig. 47. The effect on the gastrocnemius and soleus e.m.g.s of landing from a 15 inch step to the ground. This is a reconstructed example, with all parameters adjusted to correspond to the overall averages of these values determined experimentally. Illustrated also are the predicted force to be experienced by the ball of the foot, and the behavior of the ankle angle, also determined by experiment. The solid bar represents the time during which the functional stretch reflex cannot occur. It consists of 15 msec. before the ankle starts to bend, and the 120 msec. functional stretch reflex time.



Fig. 48. The predicted response of the gastrocnemius-soleus muscles to a sub-maximal stimulus to their efferent nerve supply The force that would be exerted by the ball of the foot on the forcetransducing platform is shown. No force would be recorded (though a small amount is probably developing) until 28 msec. after the start of stimulation. Maximal contraction for that level of stimulation is reached in 157 msec. stretch reflex, it would also be logical to expect the start of e.m.g. activity to be independent of the height of the step, as well as occurring after landing. It should start at the same time relative to landing in all cases; the degree of activity should vary with the height (and hence, velocity) of landing, and possibly, the activity would be prolonged when required to oppose a greater perturbance. In fact, the system is apparently quite different (Figures 25 to 30). At lower heights, e.m.g. activity starts significantly later, and maximum e.m.g. activity occurs significantly later. With higher steps, this is less apparent. E.m.g. activity ends at the same point regardless of the height of the step. (No significant difference shown.)

110

The conclusion that the stretch reflex does not function in the control of the landing from a single step is thus inescapable, and we must assume that "higher centres", which are capable of predicting what sort of muscular response is required, and sending it off in advance of landing, are responsible. Indeed, the ankle starts to extend almost 400 msec. before landing, presumably to allow a greater distance in which to decelerate the body as the ankle flexes, and this is indicative of how far in advance these "higher centres" start planning each landing.

In any case, the burst of e.m.g. activity must be responsible for the force exerted on landing, and the relation between these should be examined more closely.

The e.m.g. activity leads the force exerted during a step to the ground. The time from the first recorded e.m.g. activity of the landing until the moment of landing is 113, 161, and 152 msec. (av. 142 msec.) in steps

of 5, 10, and 15 inches respectively (Table 5). The time from maximum e.m.g. activity to maximum force exerted is 183, 162, and 125 msec. (av. 157 msec.) in steps of 5, 10, and 15 inches respectively. (Subtracting Figure 30 from Figure 25). And, the time from the moment of contact until the end of the e.m.g. burst of landing is 148, 115, and 131 msec. (av. 131 msec.) in steps of 5, 10, and 15 inches respectively (Table 5). It should be noted that forces exerted by the gastrocnemius - soleus muscles could only be recorded after landing on the force-transducing platform during steps. It was found that 27.7 msec. elapsed between the first e.m.g. activity in the gastrocnemius and its earliest mechanical response (Table 3). This means that the muscle started to contract weakly 28 msec. after the start of the first e.m.g. activity, before landing. However, the delay until maximum contraction for that degree of muscle excitation was about 157 msec., 5.6 times as long. Thus, if a stimulus were applied to the nerve supply to gastrocnemius in an intact human subject, the muscle could be expected to respond as in Figure 48.

This can be compared to the results obtained by Cooper and Eccles (1930) (Table 1). They defined the contraction time as being the interval between the onset of the electrical response and the attainment of maximum tension in the muscle. The approximate contraction time of soleus was found to be 100 msec., and that of gastrocnemius (medial head) 40 msec., in the cat. In both muscles, the mechanical contraction started almost immediately after the start of the electrical response in the preparation, suggesting that the 28 msec. lag from first e.m.g. to first mechanical response described here is at least in part due to insensitivity of the recording apparatus. The long contraction time is suggestive of slow-type muscle fibres being used in landing from a step to the ground.

112

It is of interest to see the nearly complete absence of e.m.g. activity at the moment when the functional stretch reflex should act. (Figures 19, 20, 21, 47). Since the presence of such a reflex after applying and maintaining a stretching force to the gastrocnemius - soleus muscles has been demonstrated, the question of reflex inhibition of this response arises. Figure 21 is particularly valuable in demonstrating a near-silent period in the gastrocnemius e.m.g. activity from 130 to 160 msec. after initial contact with the ground in landing from a step. This silent period was typical of most records, though the hump of increased e.m.g. activity following was not always present. How does this decrease in activity come about? It has been demonstrated earlier (Table 4) that the time from initial contact with the ground until the end of the burst of e.m.g. activity associated with landing (the beginning of the silent period) is independent of the height of the step. Thus, it appears to be related to the beginning of the stretch applied to the gastrocnemius soleus muscles. The long-loop reflex has been mentioned previously in this thesis. (Eccles, 1966). Magladery (1955) has similarly plotted H reflex excitability after a conditioning volley to the muscle afferents. What he found is illustrated in Figure 49.

The hump of increased excitability starting to rise at 120 msec. and peaking at about 300 msec. is apparently due to a long-loop-type reflex, and may contribute to the functional stretch reflex as described in this thesis.





Fig. 50. The effect on the gastrocnemius and soleus e.m.g.s of landing from a hop at the subject's preferred frequency. This is a reconstructed example, with all parameters adjusted to correspond to the overall averages of these values determined experimentally. Illustrated also is the predicted force to be experienced by the ball of the foot, also determined by experiment.

Fig. 49.

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Fig. 49. Graph showing H-reflex excitability after a conditioning volley to the muscle afferents. The percentage of normal excitability is plotted against the time after the conditioning volley to the same afferent nerve. (After Magladery, 1955).



Fig. 50. The effect on the gastrocnemius and soleus e.m.g.s of landing from a hop at the subject's preferred frequency. This is a reconstructed example, with all parameters adjusted to correspond to the overall averages of these values determined experimentally. Illustrated also is the predicted force to be experienced by the ball of the foot, also determined by experiment.

However, the H-reflex is still relatively depressed following this hump, and the possibility that the silent e.m.g. period (following the pre-programmed landing burst of e.m.g. activity) may be due to this cannot be ruled out.

The pattern of force exertion also depends on the height of the step. As it gets higher, maximum force and maximum rate of change of force occur sooner after landing, the maximum force increases, mainly in the case of small steps, and maximum rate of change of force increases, mainly in the case of greater steps.

It was significant to see that soleus behaved in a roughly similar way to gastrocnemius in stepping movements. If the stretch reflex were functional, soleus would be expected to show the results even more than gastrocnemius, as it has more spindles, is a slower muscle, and hence should be more responsive to stretch. However, in actual fact, it seems less important than gastrocnemius in a voluntary step, contracting for a shorter period of time, and having its maximum e.m.g. activity too late to contribute much to the peak force attained in landing.

Let us now turn our attention to the way in which repetitive movement (hopping up and down at one frequency) is controlled. Again, for purposes of clarity, Figure 50 is a reconstructed example of the average response to be expected during a single hop at the preferred frequency.

It is quite evident that control of a hopping movement is not the same as control of a single step. While hopping, the force exerted by the ball of the foot builds up and falls off in a smoother, more symmetrical, manner. It reaches peak values at a later time after contact, and the magnitude of the •

force is somewhat less. To change hopping rate, the time from contact to maximum force is altered. The time from contact to maximum rate of change of force, and the magnitudes of the maximum force and maximum rate of change of force do not change significantly, however. The pattern of e.m.g. activity in the gastrocnemius muscle during hopping is quite different from that during stepping. It commences later and continues for much longer, as well as being more or less constant in level, rather than in the form of a spindle-shaped burst. Also, in more than one -half of the subjects, a synchronized, biphasic discharge, apparently representing the monosynaptic reflex, was detectable in the e.m.g. at about 47 msec. after contact. E.m.g. activity in gastrocnemius tended to be greater after this point, and, in the case of soleus, almost all activity followed it. Activity in soleus tended to start later than in gastrocnemius, and end later as well. It was quite significant in amount, in contrast to the lesser amounts recorded in stepping movements. To alter hopping frequency, the e.m.g. activity in both muscles was shortened or prolonged as required. This was done entirely by changing the time from contact with the ground to the end of the electromyographic activity, since the time from the start of e.m.g. activity to contact did not change significantly.

The above is suggestive that the stretch reflex may play a more significant role in repetitive movements of this sort. The presence of the monosynaptic response and the predominance of activity following rather than preceding it, and the larger part played by soleus, all give evidence of this. E.m.g. activity still starts before contact with the ground; however, it starts
later than it would in a step of equivalent height. This lead could be due to a pre-programming of the landing, or it could now be due to a phase advancing of activity by the cerebellum, as the repetitive quality of the motion makes it predictable. The ability of all subjects to set themselves in oscillation (hopping) at a very constant frequency without outside cues is also suggestive of a feedback loop with a delay in it and the stretch reflex mechanism is the obvious one to consider. The oscillation tendency of the stretch reflex loop has been pointed out by Glaser and Higgins (1965), in their discussion of cerebellar influences on stretch reflex responses; they also suggested the muscle activity phase advancing properties of the cerebellum would tend to stabilize it. It is possible that the cerebellum is able only to maintain a delicate state of stability, which can easily be upset, resulting in hopping, or, possibly, running, movements. Each landing thus initiates the next upwards movement by means of a stretch reflex. Destabilization may occur on a strictly voluntary basis, or may be aided by an external cue tuned to the natural oscillation frequency (2.05 c.p.s.), such as the constant beat in music. Perhaps the natural frequency of running may be set in a similar way.

Sudden falls involve a complete failure of the control mechanism to predict the moment of landing on the ground. Faced with this prospect, the body responds by contracting the leg muscles as soon as possible in a general manner. Thus, no matter what the length of fall (up to one foot), e.m.g. activity is seen to start 75 msec. after the start of the fall. This delay, though small, leads to interesting consequences, as demonstrated in Figure 41. The fall of 2.3 inches caused greater forces to be applied to the foot than the fall of 8 inches. Subjectively, the lesser fall also produced a much more uncomfortable jolt. This was due to the subject's toes hitting just asse.m.g. activity was getting under way. It was insufficient to slow him down rapidly, and hence, his heel struck the platform about 50 msec. afterwards. This caused the deceleration forces to be transmitted via the solid bony column from his heel to his hip, and beyond, resulting in a greater transient load.

117

The origin of this 75 msec. "dropping reflex" is uncertain, though it may be the utricular and/or saccular maculae of the vestibular apparatus. These organs are capable of sensing downwards acceleration, and the vestibular apparatus and vestibular nuclei are known to be closely connected to brain stem areas that can control muscle activation. The reflex is too rapid for a voluntary response, and is even faster than a functional stretch reflex, which tends to eliminate peripheral receptors acting via the cord end back out to the required antigravity muscles. Of interest is the fact that the reflex activates both flexors and extensors of the ankle at the same time. Figure 41 demonstrates this phenomenon, though not so strikingly as many other records obtained. A similar situation holds in the case of voluntary wrist movements in the monkey, as shown by Evarts (1968).

Figure 43 includes a graph of maximum force attained during landing against height of fall. Force was shown to increase, decrease, and increase again as the falls become progressively greater. The hump in the curve at 4 inches may be explained by combining the effects of increased 117

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height of fall, and the reflex muscle contraction at 75 msec. described above. Short duration falls (up to 100 msec.: 75 msec. plus 27.7 msec. between electrical and mechanical events in muscle, as shown) do not allow a muscle contraction to occur. Up to this point, the force depends on the height of fall, and, thus, velocity of landing. After 100 msec., the person becomes more and more prepared to land, eventually being able to predict the moment of landing correctly, so that by 4.5 inches, the force is actually decreasing, not regaining its former level until at least 7 inches. After this point, the velocity of landing is getting quite high, and since the legs must decelerate the body in a limited distance, maximum deceleration forces increase.

A fall, then, is a failure of voluntary muscle control. Being unable to bring the normal and more accurate mechanisms into play quickly enough, and since a stretch reflex would also not be quick enough, the body is forced to activate the antigravity muscles in a non-specific manner, using the vertical acceleration sensing capability of the vestibular apparatus as a trigger.

The last part of this project was an attempt to see how the vestibular apparatus may influence antigravity muscle activity. Subjects were oscillated in a vertical, linear, fashion, and rotated about their feet and heads. If the vestibular apparatus is capable of affecting gastrocnemius – soleus muscle activity, the e.m.g. frequency should be altered (modulated) during the oscillation cycle, as long as the head has a vertical, linear, acceleration being applied to it. However, rotational acceleration could

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also be picked up by the semicircular canals and this could affect the muscle response. (Indeed, it has been shown that rotation influences the size of the monosynaptic response in gastrocnemius – soleus.) Therefore, three types of oscillation supplying vertical, linear acceleration only, rotating about the head supplying a rotational stimulus only, and oscillation about the feet producing the sum of the two effects. The records were analysed as described and three-point averaging was performed on the e.m.g. frequency versus position in cycle graphs to aid in the determination of the point of maximum e.m.g. activity.

The results, typified by Figure 45, and summarized in Figure 46, were not conclusive. Modulation was certainly present to a substantial degree. However, it was apparent in all three types of oscillation, and could be maximal in any of the three depending on the subject. There was also no correlation demonstrable between the point of maximum activity and position in the cycle. According to the work of Walsh (1961), who investigated the phase shift of sensation of position during linear vertical acceleration, there would be no phase shift in our range of 0.5 to 1.0 c.p.s. Meiry (1966) felt that subjective sensation of velocity should lag by 65 to 75 degrees in this range, however. Hence, one would at least expect the point of maximum e.m.g. activity to stay roughly in the same position in the cycle for each subject independent of mode of oscillation. Unfortunately, the results cannot be used to confirm or deny this possibility, nor do they allow us to state whether the vestibular apparatus has an effect on activity in the leg antigravity muscles.

In general, then, voluntary control of steps is apparently on the

119

the basis of pre-programmed units that are fired off centrally well in advance of landing. This is necessary because the stretch reflex response is too slow. These impulses may go directly to the a motoneurones, or they may exercise their precise control via the 8 loop. This packaging of activity may have broad applications in a multitude of quick actions such as writing, speaking, driving, flying, and many sports. Learning a physical skill may thus be seen, at least in many instances, as the setting up, or programming, of the bank of types of movements required. A new environment requires new programs, and this includes when a person first learns to walk, when first flying, or when subjected to a weightless environment. Here, the old programs are inappropriately matched to the new state, resulting in extra work to perform the same task, as continual visual and other feedback are required for control.

Repetitive leg movements may involve the functional stretch reflex in the antigravity muscles of the leg as well as a pre-set landing program. Each landing from a hop may be accomplished in a manner similar to that of a single step (i. e., a precise, pre-programmed signal package released centrally well before landing by visual and other cues.) This may be followed by a functional stretch reflex, which would act in such a manner as to launch the body into the next hop. The functional stretch reflex may correspond to the rise, and subsequent hump, of "H-reflex" excitability starting 60 to 110 msec. after commencing muscle stretch. The start of the e.m.g. activity of the next landing from a hop may in part be due to the imposition of weightlessness on the body, similar to a sudden fall, with reflex e.m.g. activity starting as demonstrated about 75 msec. later. The setting of a preferred hopping frequency may be on the basis of this frequency being the one at which the "fall reflex" and the start of the desired landing program for that hop most closely correspond in time (see Figure 51). This summation of the two effects, plus the best possible timing of the functional stretch reflex, may result in the body oscillating at that frequency, and it may be further driven by an external source, such as a synchronous, repetitive, auditory cue. The way in which the beat of much current music centres about this frequency is interesting indeed, perhaps explaining the form of some modern dances.

121

If a movement is unpredictable, such as a fall, voluntary control fails, and a (vestibular?) reflex automatically contracts the leg muscles to protect the body against sudden shocks. However, the necessary, though small, delay in this system means that falls of under 3 to 4 inches do not allow significant muscle contractions to develop before impact, so that the heel inevitably strikes the ground, and large transient forces are transmitted up the skeleton. This gap in which voluntary control is not present and the reflex response has not occurred perhaps explains the very disrupting effect of a higher or lower step in a set of stairs, or an unexpected step down an unseen curb.

The high forces resulting could cause fractures, for example, of the ankle, or of the neck of the femur, expecially in the older person. Perhaps this feature accounts for the fact that Pott's fractures (of the ankle) are the second commonest type encountered in man.

A successful stepping movement requires accurate timing, as



## Fig. 51.

Diagram of the average electromyographic activity in the gastrocnemius-soleus muscles (EMG) and the force exerted by the ball of the foot (F) during 2 repetitive hops at the average preferred, too fast, and too slow frequencies. The diagrams are intended to accurately represent the timing of these responses relative to the moment of contact with the ground ("C") only; all values used are the averages for the eight group I subjects. The time from the moment of leaving the ground in a hop until the e.m.g. activity concerned with landing from that hop was calculated to be 70, 50, and 100 msec. in hops at the preferred, too fast, and too slow frequencies respectively.



Fig. 51.

122

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Diagram of the average electromyographic activity in the gastrocnemius-soleus muscles (EMG) and the force exerted by the ball of the foot (F) during 2 repetitive hops at the average preferred, too fast, and too slow frequencies. The diagrams are intended to accurately represent the timing of these responses relative to the moment of contact with the ground ("C") only; all values used are the averages for the eight group I subjects. The time from the moment of leaving the ground in a hop until the e.m.g. activity concerned with landing from that hop was calculated to be 70, 50, and 100 msec. in hops at the preferred, too fast, and too slow frequencies respectively.



demonstrated, and also correct magnitude of contraction. This could be set by the vestibular apparatus while falling, but whether this actually occurs or not is uncertain.

## SUMMARY

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Surface electromyograms from human calf muscles, and the force exerted by the ball of the foot, were recorded during steps, repetitive hopping, and unexpected falls.

An attempt was made to measure the latency of the functional stretch reflex in the leg as well, by the subject resisting an applied and maintained dorsiflexing force to his foot.

3. Subjects were also oscillated in a vertical, linear, manner, and the gastrocnemius e.m.g. was analysed to find any modulation due to vertical accelerations.

4. It was found that forces exerted are of lesser magnitude, and change less abruptly, if the moment of landing of the foot is more precisely predictable.

5. E.m.g. activity in a step is half over before contact is made with the ground. No monosynaptic discharge is seen, and all activity is over before a functional stretch reflex could add anything to it.

While the subject hops at his most natural frequency, the e.m.g.

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starts before contact and often shows a monosynaptic burst 50 msec. after contact. Most e.m.g. activity falls after this spike, and it continues for several hundred msec.

While falling, voluntary control fails, and e.m.g. activity starts 74 msec. after the start of downwards motion, regardless of the height of fall.

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Vertical oscillation of subjects produced a modulation of the gastrocnemius – soleus e.m.g. activity. Peak activity did not correlate with frequency of oscillation, and the mechanism behind the modulation is uncertain.

It is suggested that the monosynaptic discharge and stretch reflex play no part in the control of the calf muscles during a single stepping movement or in a short fall, but they may have a function in hopping and running.

10. The normal mechanism during stepping appears to function on the basis of pre-programmed activity sent off from higher centres at the precisely correct moment, before contact is made with the ground.

To prove that if an individual steps down 1 foot, and if his functional stretch reflex in a muscle takes 120 msec., he will fall over 14 inches farther before being able to produce any electromyographic activity in that muscle:

Assume he has fallen 1 foot. The time taken to do this is:

S	=	$v_{o}t + \frac{1}{2}at^2$
1	÷	$\frac{1}{2} \times \frac{32}{2} \times t^2$
t	=	.25 sec.

Now add 120 msec. functional stretch reflex time:

t = .25 + .12 = .37 sec.

At 0.37 sec. after start of downwards motion,

S = 
$$\frac{1}{2} \text{ at}^2$$
  
=  $\frac{1}{2} \times \frac{32}{2} \times \frac{(.37)^2}{2}$   
= 2.19 feet

During the 120 msec., he has travelled:

$$2.19 - 1 = 1.19$$
 feet = 14.3 inches

This solution requires the subject to be falling freely, and is an ideal case.



In a downwards and forwards step of 1 foot, the subject does very little in the way of letting himself down, and so this quite closely approximates the true value.

A



## **APPENDIX 2**

Statistical methods:

$$\frac{\text{Standard Deviation}}{\text{Standard Deviation}} = \sqrt{\frac{\Sigma(x-\overline{x})^2}{n-1}} \qquad \text{where } x = \text{individual value} \\ \overline{x} = \text{average value} \\ n = \text{number of} \\ \text{observations} \end{cases}$$

$$\frac{\text{Standard Error}}{\text{Standard Error}} = \frac{\text{Std. dev.}}{\sqrt{n}} \qquad \text{where the S. D. is determined} \\ \text{as above, and n is the number} \\ \text{of observations.} \end{cases}$$

$$\frac{\text{'t'' test:}}{\sqrt{(\text{SE}_1)^2 \cdot \frac{N_1 - 1}{N_2} \cdot g} + (\text{SE}_2)^2 \cdot \frac{N_2 - 1}{N_1} \cdot g}$$

where 
$$g = \frac{N_1 + N_2}{N_1 + N_2 - 2}$$

x = mean

SE = standard error of mean

N = number of observations

NOTE: if N<sub>1</sub> = N<sub>2</sub>  

$$t = \frac{\overline{x}_{1} - \overline{x}_{2}}{\sqrt{(SE_{1})^{2} + (SE_{2})^{2}}}$$

<u>"P" value</u>: derived from a table of the distribution of "t" compiled by Student.

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