MOTOR UNIT ACTIVATION IN UNILATERAL AND BILATERAL MUSCLE CONTRACTION IN MAN

©

by

Anthony A. Vandervoort, B.Sc.

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Master of Science

McMaster University

MASTER OF SCIENCE
(Adapted Human Biodynamics)

McMaster University
Hamilton, Ontario

TITLE: Motor Unit Activation in Unilateral and Bilateral Muscle Contraction in Man.

AUTHOR: Anthony Allan Vandervoort, B.Sc. (University of Waterloo)

SUPERVISOR: Professor D. G. Sale

NUMBER OF PAGES: viii, 102, Appendix

ABSTRACT

The present study was undertaken to investigate the mechanism underlying the observation that the maximal voluntary strength of the two legs acting together or bilaterally in isometric leg extension was less than the summed unilateral (sum of the left and right legs tested separately) strength. Observations were made on this phenomenon under both isometric and concentric contraction conditions by testing young adult males performing unilateral and bilateral leg press contractions on a modified isokinetic dynamometer.

Electromyographical evidence indicated that there was a lesser activation of motor units in bilateral contractions, as compared to unilateral, under isometric conditions and at a low and high concentric velocity. To determine whether a particular type of motor unit was being activated to a lesser extent in bilateral contractions, two physiological parameters of unilateral and bilateral contractions were compared: the strength-velocity relation and fatigability. This investigative method was based on the known physiological differences between the motor unit types; namely fast-twitch (FT), type two motor units have a faster twitch contraction time, greater force output at high velocities of shortening and lesser resistance to fatigue than the slow-twitch (ST), type one units.

Results showed a greater relative decline in the strength of bilateral contractions as the velocity of contraction was increased through a range from 0°/s to 424°/s (0 to 7.40 radians/s). The

bilateral to summed unilateral strength ratio (B/U ratio) decreased from 0.91 under isometric conditions to 0.51 at the highest test velocity. Lesser fatigability was found in the bilateral condition in a 100 consecutive concentric contraction fatigue test. These results provided complementary evidence for the conclusion that FT motor units were active to a lesser degree in bilateral contractions.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. D. G. Sale for the enthusiastic advice and encouragement I have received during the course of this investigation. Thanks also are extended to Dr. J. S. Frank and Dr. B. A. Gowitzke for their contributions to the preparation of this thesis.

I also wish to thank Mr. John Moroz for his technical assistance throughout the project and Ms. Phyllis Koetting for typing the thesis.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

I. INTRODUCTION

A. Purpose and Scope of the Investigation

It has been observed (Secher et al., 1978) that the maximal voluntary strength in an isometric leg extension movement when the legs acted together, or bilaterally, was less than the summed unilateral strength (sum of the left and right limbs tested separately). The purpose of the present study was to investigate the underlying mechanism responsible for this bilateral strength deficit. First, electromyographical (EMG) methods, which had not been previously utilized, were used to determine if there was a lesser activation of available motor units during bilateral contractions. This was done under isometric conditions, and additionally with concentric contractions, thus expanding the investigation of this phenomenon to include dynamic efforts.

Second, physiological studies were undertaken to determine if a particular type of motor unit was undergoing lesser activation during bilateral contractions. Secher et al. (1978) had used a drug-blocking technique to selectively inhibit slow-twitch (ST), type 1 or fast-twitch (FT) type 2 motor units during unilateral and bilateral contractions, to examine this question. Although they concluded there was ST motor unit inhibition in the bilateral condition, their results were not consistent between the drug manipulations (see Discussion). Another possible approach to this problem is to observe the pattern of glycogen depletion from the two muscle fibre types, for evidence of a greater usage in one or the other. This approach would require the use the invasive technique of muscle biopsy sampling however. Furthermore, the technique might not be a reliable indicator of motor unit recruitment for the short duration exercise used in this study (Gollnick et al., 1980).

The investigative method used to examine this question in this study was as follows. There are known physiological differences between the two motor unit types; namely FT units have a faster twitch contraction time, greater force output at high velocities of shortening and lesser resistance to fatigue (for review see Burke and Edgerton, 1975; also Thorstensson, 1976; Buchthal and Schmalbruch, 1980; Gollnick et al., 1980; Tesch, 1980). It was reasoned that differences in the amount of activation of a motor unit type between unilateral and bilateral contractions could be investigated by comparing the strength-velocity relation and fatigability of the two types of contraction. For example, if fast-twitch motor units were activated to a lesser extent in bilateral contractions than unilateral, there would be an expected greater relative decline in strength when the velocity of contraction was increased, and an expected greater resistance to fatigue during sustained or repetitive contraction. In this manner, these two aspects of muscular contraction, strength-velocity relation and fatigability, were observed for unilateral and bilateral contractions, to provide complementary evidence of a greater activation of a motor unit type in one condition and not the other.

B. Review of Literature

1. Unilateral and Bilateral Strength Performance. It has been previously reported in the literature several times that the

maximal voluntary strength of the two legs acting together, or bilaterally, in isometric leg extension was less than summed unilateral strength (Secher, 1975, Secher et al., 1976, 1978; Rube et al., 1979; and as reported in Secher et al., 1978; Asmussen et al., 1959 and Asmussen and Heeboll-Nielsen, 1961). This bilateral deficit in strength has also been demonstrated in a weight-lifting leg press movement (conclusion of unpublished study by G. Moran, shown to writer by Dr. D. Sale in a personal communication). The ratio of bilateral to summed unilateral strength (B/U ratio) was approximately 0.75 in Secher et al.'s (1978) investigation of this phenomenon, but Secher (1975) has presented evidence that this ratio may be higher in subjects who have had extensive bilateral strength training experience. In persons who had not had this training however, there appeared to be a significant bilateral deficit in strength, according to Secher's studies.

Secher's findings suggest that those subjects who were achieving B/U strength ratios of less than unity, were not obtaining as full an activation of the available motor units of the involved muscles in bilateral as compared to unilateral muscular contraction. The highly trained oarsmen which Secher (1975) tested as representatives of athletes who had undergone extensive bilateral strength training would appear to have been able to overcome this problem, thereby achieving higher B/U strength ratios. This work suggests that there is some sort of mechanism responsible for this bilateral strength deficit that can be modified by strength training, as was shown in a weight training study (see the above personal communication). Possible mechanisms and their implications for unilateral and bilateral muscular contraction are the subject of this review of literature.

2. Possible Mechanisms Responsible for the Bilateral Strength Deficit. It is possible that the addition of the second limb to a unilateral muscular contraction decreases the level of excitation of the spinal motoneuron pool of the involved muscles of that limb. This would decrease the activity of the motor units and hence the strength of the contraction. To the author's knowledge, this has not been investigated using electromyographical methods. Decreased motoneuron excitability could be due to an increase in the inhibitory input to the spinal motoneuron pool and/or a decline in the excitatory input, thus decreasing the activation of some of the motoneurons. Motoneuron activation is dependent upon the attainment of a critical amount of depolarization of its cell body membrane, that will trigger an action potential (Guyton, 1976:68). Possible sources of changes in these inputs are discussed below.

(a) Influences on the spinal motoneuron pool in a bilateral muscular contraction. Evidence of peripheral neural communication between limbs has been demonstrated in the spinal animal (for review see Hunt and Perl, 1960; Stein, 1974). One example is the crossed extensor reflex, which is elicited by applying a noxious stimulus to a limb (Sherrington, 1906). It involves initiation of a flexion response of the involved limb in order to withdraw it from the stimulus, and also an initiation of extension in the contralateral limb, supposedly to push the body away from the danger (Guyton, 1976: 135). Concommitant with these effects are an inhibition of antagonist muscles that permits the movement to occur without interference. This includes the extensors of the involved limb and flexors of the contralateral limb.

It has been reported that a myotatic reflex pattern, similar to the crossed extensor reflex, may be responsible for enhanced muscle strength in a bilateral movement in which one limb was in flexion and the other in extension (Hellebrandt et al., 1951; Provins, 1955 and Morris, 1974), as compared to when the limbs were tested separately. In the latter study by Morris (1974), the muscle spindles of one leg were stimulated by imposing a flexion stretch on it as it was undergoing isometric knee extension in a maximal voluntary contraction (MVC). An increased strength was observed in the other leg which was undergoing isometric flexion MVC. In a parallel experiment by Lagasse (1974), in which both legs were undergoing isometric knee extension MVC and this flexion stretch was superimposed on one leg, the strength of the contralateral leg decreased. Both Morris (1974) and Lagasse (1974) interpreted their findings as evidence for a reflex pathway between the two limbs that was consistent with the crossed extensor reflex. The postulated stimulus for the reflex was the activity of the muscle spindles which were activated when the stretch was imposed on the leg.

The isometric bilateral leg extension condition used in Secher et al.'s (1978) study involved a similar type of contraction in both limbs, as opposed to flexion in one and extension in the other. It would appear that there was a potential source of inhibition arising in each limb and crossing to the other that could stem from cutaneous receptors activated as a result of the contraction. Also, spindle afferents could be activated that affect the opposite limb, when the spindles are stimulated by gamma coactivation occurring in the muscle contraction along with the alpha motoneuron excitation (Granit, 1970).

What may also be of importance, along with this spinal communication between the two limbs, is the fact that in a bilateral muscular contraction involving the same muscles in each limb, the crossed extensor reflex type of circuitry cannot be utilized by the central nervous system (CNS), but rather a different pathway must be taken to activate the motoneurons. This could cause an incomplete activation of the available motor units in subjects who are not familiar with exerting maximal voluntary forces in bilateral leg extension. The neuromuscular system may be better suited for muscular contraction in which reciprocal innervation patterns are used such as in walking (Easton, 1972).

The attainment of a high level of skill in a movement seems to involve the development of inhibition of unwanted reflex arcs affecting the motoneurons (Clough, 1971; Basmajian, 1977), while facilitating other reflex arcs that are important (Hayes and Clarke, 1978). An increased facilitation of the motoneuron pool following a program of resistance training has recently been demonstrated by Sale (1979) as a mechanism for strength gains following training. It could be that this type of facilitation also occurs in the pathways for bilateral muscular contraction during bilateral strength training, and even perhaps as the result of the unilateral strength training as outlined below.

(b) <u>Cross-transfer of training effect to the contralateral limb</u>. Many studies on the effects of resistance training on muscle strength have noted a significant increase in the voluntary strength of the homologous muscle(s) of an unexercised limb when the other limb was trained (Hellebrandt *et al.*, 1947; Slater-Hammel, 1950;

Hellebrandt, 1951; Mathews et al., 1956; Logan and Lockhart, 1962; Awad and Kottke, 1964; Coleman, 1969; Shaver, 1970; Smith, 1970; Shaver, 1973; Imms et al., 1977; Moritani and DeVries, 1979). The mechanism for these cross-transfer effects of training has not yet been identified. Hellebrandt et al. (1947) advanced one theory that the body experiences widespread excitation of muscles in order to stabilize the body to support the contracting limb. There is thus efferent activity going from the CNS to both the exercising limb and the contralateral limb.

Although the contralateral homologous limb muscle has been shown to exhibit some EMG activity during the contraction of the opposite limb, this activity was small in comparison to the trained limb (Moore, 1975). With this small magnitude of "overload" activity to stimulate muscle adaptation, the unexercised muscle would not be expected to undergo any significant increases in muscle size, biochemical activity or contractile protein during strength training of the opposite limb. Moritani and DeVries (1979) reported an increase in the unexercised arm strength after strength training of the opposite limb, but found no increase in muscle size, as measured by limb girth minus estimated skin and fat. These authors postulated that the strength increase was due to changes in the ability of the central nervous system to voluntarily activate motor units.

It has been previously suggested that the untrained individual under normal circumstances does not maximally activate the motoneuron pool during a maximal voluntary muscle contraction, as it has been shown that hypnosis or external stimuli like shouts or gunshots can be used to increase subjects' maximal strength (Roush, 1951; Ikai and Steinhaus, 1961). The increases in MVC in the unexercised limb due to a cross-transference of training may also be a reflection of an increased ability to activate motor units, possibly because of adaptation in the supraspinal pathways. Some indirect evidence that this adaptation would be supraspinal, comes from the work of Hellebrandt (1951), Walters (1955), and Hellebrandt and Waterland (1962), who found that motor skill learning can occur in one limb as a result of the opposite limb's training. This suggested an involvement of the higher centres of the brain in establishing a complex movement pattern in the contralateral limb.

Part of the cross-transference effect then may be due to the establishment of a pathway in the CNS for the activation of motor units in the unexercised limb, thereby increasing its strength. As the brain output for the two limbs is arising at the same time, in a similar manner to a bilateral muscular contraction, it might be postulated that unilateral strength training could improve bilateral strength, if the bilateral deficit in strength in untrained individuals was due to a failure of the CNS to fully activate the motoneuron pool relative to the unilateral contractions. Unilateral isometric strength training of leg extension has recently been shown to increase the isometric B/U leg extension strength ratio by Rube <u>et al.</u> (1979). To the author's knowledge a similar study has not been done in regard to dynamic strength training.

(c) Unilateral muscular contraction. It has been suggested above that even when only one leg is called upon to contract there may be some involvement of the other leg. Yet, it seems logical to assume that the "mental energy" (Brodal, 1973) or concentration that is required for a unilateral muscular contraction is better directed towards that limb, than when there are two limbs on which to divide the attention. This argument refers not only to the initial stage of the muscular contraction in which the alpha spinal motoneuron is activated, but also to the constant monitoring of feedback regarding the muscular contraction that occurs (Matthews, 1972).

That is, there arises from the receptors of the contracting limb several sources of activity, including muscle spindle activity which appears to be excitatory to the contracting muscle; and activity from the Golgi tendon organ which appears to be inhibitory (Henneman, 1974). Also, sensory activity from other tissue receptors, such as the skin, which may be activated as a result of the contraction, could be inhibitory to an extension movement in a limb if the flexor reflex is stimulated (Guyton, 1976: 133).

The reflexes arising from the muscle spindle and Golgi tendon organs are generally thought to be used by the motor system to produce a smooth, rather than jerky development of muscular force (Easton, 1972). In fact, the sensitivity of the muscle spindle appears to be under central nervous system control, such that the effect of the feedback loop, as in a tendon tap procedure, on the force of the muscular contraction involved, can be modified (Stein, 1974). To the author's knowledge the relative importance of pain reflexes to a maximal voluntary contraction is unknown.

One factor which may have an important bearing on the effect of reflexes and sensory feedback loops is that of the duration of the contraction. In a brief voluntary muscular contraction that is ballistic in nature, in which the task involves a largely preprogrammed chunk that is performed without regard to sensory feedback (Desmedt and Godaux, 1979), the input of the reflexes discussed above may be minimal (Desmedt and Godaux, 1979; Maton, 1980). Thus, in the situation where the strengths of unilateral and bilateral muscular contraction in a high velocity ballistic condition are compared, any differences in strength might be attributed to differences in the central preprogrammed commands for motor unit activation (assuming there are no other differences affecting the strength of the contractions, such as instability in one condition and not the other).

To the author's knowledge a study comparing the strength of unilateral and bilateral muscular contractions under high velocity dynamic conditions has not been reported in the literature. Nor, as reported earlier, has an electromyographical study of motor unit activation in unilateral and bilateral muscular contraction been reported. However, if an assumption is made that there was a lesser activation of motor units in the bilateral muscular contraction, thereby causing the bilateral deficit in strength, the question arises as to which type of motor unit was undergoing lesser activation in bilateral efforts, slow-twitch or fast-twitch.

3. <u>Activation of Motor Units in Unilateral and Bilateral Muscular Contraction.</u>

(a). <u>Motor unit types</u>. It should be noted at this point that, for the purpose of this investigation, only two types of motor units will be considered, slow-twitch or type I and fast-twitch or type II. Presently, at least three different human muscle fibre types can be identified, based on their histochemical staining properties for myosin ATPase activity (Brooke and Kaiser, 1974; Saltin et al., 1977; Houston, 1978; Gollnick et al., 1980); two of which are designated fast-twitch subtypes and one which is slow-twitch. However, in much of the literature pertinent to this investigation only a two-fibre muscle classification scheme, slow-twitch and fast-twitch was used. In this scheme muscle fibres are separated into two groups, one that has a relatively slow develompent of tension and the other, faster contractile properties. The FT muscle fibre can make and break the tension generating cross-linkages between the actin and myosin filaments of its myofibrils at a faster rate than the ST muscle fibre, partly because of greater myosin ATPase activity (for review see Close, 1972; Burke and Edgerton, 1975; Edgerton, 1976; Gollnick et al., 1980). In this latter scheme the two fast-twitch fibre sub-types referred to above are considered together. It has been shown that human muscles are composed of varying proportions of FT and ST fibre types (Johnson et al., 1973, Burke and Edgerton, 1975).

Another reason for using this two motor unit scheme (it should be noted that it has been demonstrated that motor units are exclusively made up of one type of muscle fibre or the other (Burke and Edgerton, 1975)) is that generally only two groups of motor units can be identified according to their twitch contraction times in electrophysiological studies (Sica and McComas, 1971; Garnett et al., 1978). The difference between the fast-twitch muscle fibre subtypes seems to be in their recruitment patterns (Grimby and Hannerz, 1979) and their capacity for oxidative metabolism (see Burke and Edgerton, 1975; Essen et al., 1975; Houston, 1978). A fast-twitch motor unit moderately resistant to fatigue and a highly fatigable fast-twitch motor unit seem to exist (Peter et al., 1973; Garnett et al., 1978).

In summary, the motor unit types discussed in the present investigation will be referred to as slow-twitch and fast-twitch. It has been observed in the past, that the slow-twitch motor unit has a slower twitch contraction time but greater resistance to fatigue than the fast-twitch motor unit due to differences between the units in contractile properties and the capacity for oxidative metabolism attributable to differences in the structure, contractile enzyme activity, metabolic enzyme activity and capillarization between the fibre types (Close, 1972; Burke and Edgerton, 1975; Essen et al., 1975; Saltin et al., 1977; Houston, 1978; Gollnick et al., 1980). There are also differences between the motoneurons of the 2 motor unit types, in that the motoneuron of the fast-twitch motor unit is reported to be larger and have a faster conduction velocity than the slow-twitch (Burke and Edgerton, 1975; Edgerton, 1975; Wolf, 1979). Further, it is generally held that the fast-twitch motoneuron cell membrane will be more difficult to depolarize to the threshold level for the firing of an action potential than the slow-twitch membrane, because its larger cell body size offers lesser input resistance to the depolarizing current generated by synaptic transmission (Henneman et al., 1965; Barrett and Crill, 1971, 1974; Desmedt and Godaux, 1979).

(b) Selective inhibition of a motor unit type in bilateral muscular contraction. It has been reported by Secher et al. (1978), that the ST motor units were being restricted during bilateral contractions, thereby causing the bilateral loss in strength. This conclusion was based on results of experiments using the drugs d-tubocurarine (dtc) and decamethonium (C_{10}) to selectively block the slow-twitch or fast-twitch motor units at their neuromuscular junction respectively. Their results were not consistent between the two drug manipulations and this conclusion seems to be based mainly on the effects of C_{10}. D-tubocurarine did not seem to alter the B/U strength ratio.

A partial inhibition of ST motor units during bilateral contractions would cause the FT motor units to make a proportionately greater contribution to the force of contraction, thereby causing the involved muscles to exhibit to a greater extent the functional characteristics associated with muscle possessing a high percentage of FT muscle fibres (% FT fibres). It has been previously demonstrated that in muscles possessing a high versus low proportion of FT fibres, the decline in strength with increasing velocity of concentric contraction is less (Thorstensson et al., 1976, 1977; Coyle et al., 1979; Gregor et al., 1979), while the rate of fatigue (fatigability) is greater (Thorstensson and Karlsson, 1976; Nilsson et al., 1977; Tesch et al., 1978c; Komi and Tesch, 1979). These findings are consistent with the characteristics attributed to the two types of muscle fibres described in a previous section of the Review of Literature. Coyle et al. (1979) have noted that in isokinetic contractions, it was not clear whether the advantage of a high proportion of FT muscle fibres is due to a greater development of peak muscular tension at a given time in the contraction, or due to a faster rate of tension development in relation to the optimum knee joint angle for peak torque production. However, Gregor et al. (1979) controlled for this latter factor, and still found the above reported effects.

On the basis of these functional characteristics associated with muscles possessing a high proportion of FT fibres, it seems reasonable to hypothesize that: (1) the decline in strength with increasing velocity of concentric contraction would be less in bilateral than in unilateral muscle contractions; (2) fatigability would be greater in bilateral than in unilateral muscle contractions. The relevant conclusion of Secher et al. (1978), that there was an activation of FT motor units during bilateral muscular contraction, while some ST units were inhibited, is contrary however to other research on isometric contraction, in various muscle groups, that suggested that ST units will always be activated whenever FT units are (Henneman and Olson, 1965; Henneman et al., 1965; Person and Kudina, 1972; Milner-Brown et al., 1973a, b; Gydikov and Kosarov, 1974; Desmedt and Godaux, 1977a, b; Garnett et al., 1978; Desmedt and Godaux, 1979).

This discrepancy can be examined by comparing the strength-velocity relation and fatigability of unilateral and bilateral muscular contraction as noted above. For example, if FT motor units were actually activated to a lesser extent in bilateral muscular contraction than unilateral, as might be expected, then the decline in strength with increasing velocity of contraction would be greater in bilateral than in unilateral muscle contractions and fatigability would be less in the bilateral condition. This logic is based upon the demonstration that human muscles have varying proportions of fast-twitch and slow-twitch muscle depending on the muscle in question and the individual

(Johnson et al., 1973; Burke and Edgerton, 1975; Edgerton et al., 1975; Gollnick et al., 1980). If, for example, the muscles involved in both unilateral and bilateral muscle contractions were all of one fibre type, differences between the strength-velocity relation and fatigability of the two types of contraction might not be expected to occur, if all other factors (such as blood flow to the limbs in each condition) were equal. Rather, one type of contraction would simply parallel the other in these two aspects of muscular contraction, but at a different level of force output.

C. Conclusion

Prior investigation of the B/U strength ratio phenomenon has been limited to isometric muscle contractions, according to published research on the topic. In the present study, this phenomenon was examined during concentric contractions at various velocities as well as under isometric conditions. An electromyographical investigation was undertaken to determine whether motor unit recruitment was decreased in bilateral muscular contraction as compared to unilateral. As well, the strength-velocity relation and fatigability of unilateral and bilateral muscular contraction were compared to provide a test of the hypotheses presented above, regarding the type of motor unit that is recruited to a lesser extent in bilateral contractions, thereby causing the bilateral deficit in strength. This study provided evidence with which the conclusion made by Secher et al. (1978), that slow-twitch motor units are inhibited during bilateral muscle contractions, could be supported or challenged.

It was anticipated that the examination of the B/U strength phenomenon under high velocity conditions, when sensory feedback pertaining to the muscular contraction was limited (Desmedt and Godaux, 1979) would provide some insight into the mechanisms responsible for the bilateral deficit in motor unit recruitment. Thus, this investigation expanded the investigation of the B/U strength ratio phenomenon to provide new directions for research as outlined below.

The study made a methodological contribution to the measurement of voluntary strength. A commonly used isokinetic dynamometer (Cybex II, Lumex Inc., Bayshore, New York) was adapted to permit bilateral testing of large muscle groups. In addition, this adaptation extended the torque capacity and velocity range of the dynamometer. A potentiometer was connected to the leg press lever arm during the adaptation of the Cybex to measure lever arm displacement in relation to torque development throughout the muscle contraction. This provided some additional information regarding the effect of changing knee joint angle on tension development in a concentric isokinetic contraction.

The protocols developed during this investigation provide a basis for future experiments relating to the underlying mechanisms responsible for the phenomenon under study. In the future, these mechanical measurements can be combined with electrophysiology and histochemistry to provide new evidence related to the pattern of recruitment of motor units during unilateral and bilateral contractions. The adapted dynamometer will also permit specific unilateral and bilateral strength training studies. These studies could explore the extent to which the B/U ratio can be altered by training and further clarify the relative roles of neural and muscle adaptation during strength training.

II. METHODS

A. Electromyographical Study of Unilateral and Bilateral Quadriceps Function in the Leg Press

1. Apparatus. Electromyographic recordings were made from the vastus medialis, vastus lateralis and rectus femoris muscles of the right leg during unilateral and bilateral muscular contraction in the leg press movement. Surface electrode sites were prepared by rubbing the skin briskly with an alcohol soaked gauze pad, to provide sufficient abrasion. Two Beckman silver/silver chloride surface electrodes with 10 mm contact diameter, filled with Beckman electrode jelly, were then attached by electrode collars to the skin over the belly of each of the above muscles, along the longitudinal axis with an interelectrode distance of 40 mm. A reference electrode was placed near the greater trochanter of the femur.

The EMG signals arising from these placements were visually inspected on a Honeywell 4-channel oscilloscope for excessive noise levels. Electrode placement was adjusted until a satisfactory signal was present. The EMG signals were amplified with Honeywell Accudata model number 135A amplifiers, using filter settings that eliminated frequencies below or above 15 Hz and 2.5 KHz respectively, and then recorded on magnetic tape (Tandburg model number series 100 FM 4-channel instrumentation recorder) at a speed of 19 cm/s. After the initial adjustment of the amplifier levels for each subject, to maximize the size of the signal being recorded, these settings were not changed throughout the series of contractions.

For analysis, the recorded EMG signals were rectified and integrated with a Honeywell Accudata integrator model number 126, before being transferred onto paper with a Honeywell Visicorder, model number 2208A oscillograph. The time constant for integration was not changed throughout the analysis of a subject's records.

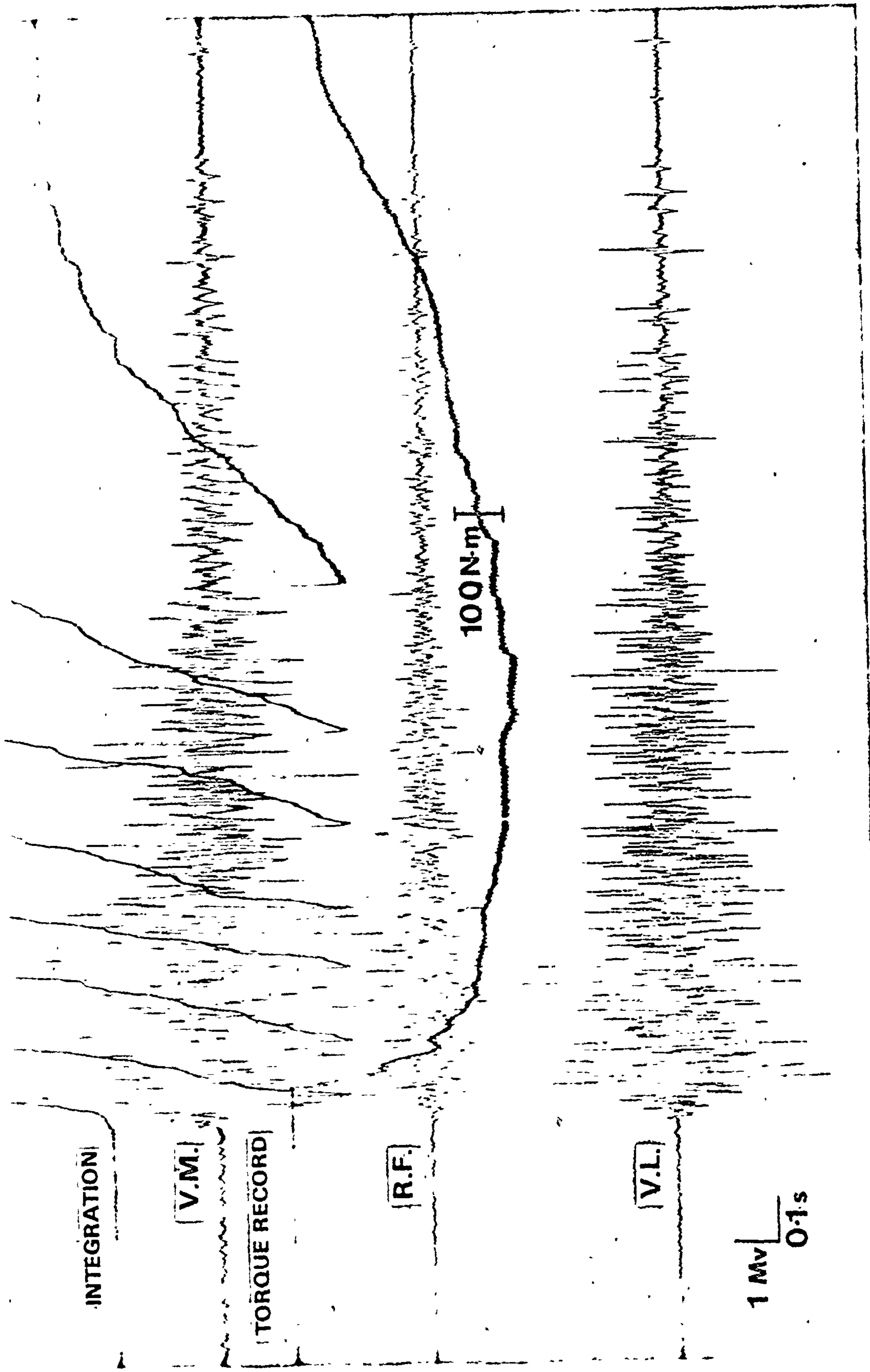
2. Procedures. The integrated EMG activity from the 3 monitored muscles of the right quadriceps was obtained during right only and bilateral muscular contractions in the leg press movement at 0°/s, 15°/s and 380°/s velocity, performed as outlined in Part B of the Methods. The order of presentation of the tests was randomized. The torque record and the record of the movement of the lever arm were recorded on channel 1 and 2 respectively of a Hewlett-Packard 7402A oscillographic recorder. Also, the torque record was stored on the fourth channel of the FM recorder in conjunction with the EMG signals. Subjects were given 3 warm-up trials and 3 MVC trials at each velocity. The trial in which the highest peak torque was produced was considered in the analysis.

The integrated EMG activity was measured in the arbitrary units of the number of sweeps of integration (Figure 1) produced over a specified time period of the unilateral and bilateral contractions at each velocity. These were as follows:

(1) For isometric contractions, for a 3 second period after the start of the integration of EMG activity

(2) For contractions at the 15°/s and 380°/s velocity, from the start of the integration of the EMG activity to the end of the torque record. Generally the

Figure 1. Example of an EMG recording in which the EMG activity of the vastus medialis muscle (upper) has been integrated. Other traces are from the rectus femoris muscle (middle) and vastus lateralis muscle (lower). Solid line is the torque record. Angular velocity of the lever arm was 15°/s.


INTEGRATION
V.M.
TORQUE RECORD
R.F.
V.L.
100N·m
1 Mv
0·1s

duration of the torque record was similar in the right only and bilateral contractions. Comparisons between the two conditions were made on an equal time basis.

The peak torque generated in the above time periods was also recorded.

3. Subjects. Subjects for this part of the study were 4 active male physical education students of similar height and weight to the subjects used in the strength-velocity and fatigue studies described later in the Methods. These subjects were not regularly participating in a weight training program at the time of the study. Their ages ranged from 23-24 years (mean was 23.3 years), height ranged from 172.7-185.4 centimetres (mean was 176.5 cm) and weight from 65.8 to 73.5 kilograms (mean was 70.8 Kg).

B. Measurement of Voluntary Strength

1. Apparatus. Voluntary strength was measured with a Cybex (Lumex Inc., Bayshore, New York) leg press training machine, modified to permit coupling to a Cybex II isokinetic dynamometer by a gear and chain system. These modifications as described below allowed the use of the Cybex II, which is designed to measure isometric or concentric contraction strength in unilateral, single joint movements, for the measurement of the torque produced by bilateral (left and right limbs acting together) multijoint movements involving large muscle groups.

The shaft of the Cybex II is mechanically prevented from exceeding the pre-set velocity when external torque is applied to it, being able to resist approximately 500 newton-metres (N.m) of torque. This torque capacity however, was insufficient to measure the larger torque produced in the leg press movement used in this study

(Figure 2). In a low velocity bilateral leg press movement, for example, the peak torque may exceed 2000 N.m. As such, a gear and chain system was used to couple the leg press training machine to the Cybex II isokinetic dynamometer that increased the torque capacity by factors of 2-5, with corresponding decreases in the velocity limit of the device, which is normally 3.67 rad/s. The system also provided for increases in the velocity limit of the dynamometer by factors of 2 and 3, with corresponding decreases in the torque capacity. The gear and chain coupling system is shown in Figure 3. The gears and chain were of a standard industrial size, bored out in the centre to allow fastening to the Cybex II shaft, or to the lever arm of the leg press.

A 10-turn potentiometer (Bourns, U.S.A., #3400S-1-203, linearity ±0.15%) was attached to the lever arm of the leg press in order to monitor the angular rotation of the lever arm throughout the leg press movement. It was also possible, using this device, to measure the angular velocity of the lever arm and compare it to the expected velocity, based on the gear system and Cybex dial setting. For example, if the gear system in use was a 4:1 ratio, of the gear on the lever arm to the gear on the Cybex shaft, and the Cybex II pre-set velocity was 60°/s, the expected angular velocity of the lever arm would be 15°/s. However the torque registered by the Cybex would only be one-quarter of that produced by the subject.

The output from the Cybex II dynamometer was displayed on a 2-channel Hewlett-Packard 7402A oscillograph recorder. Figure 4A shows a sample recording from the recorder. The display on channel one was a record of the torque production and permitted the measurement of peak torque in newton-meters. The second channel displayed the

Figure 2. Leg press apparatus used to measure voluntary strength.

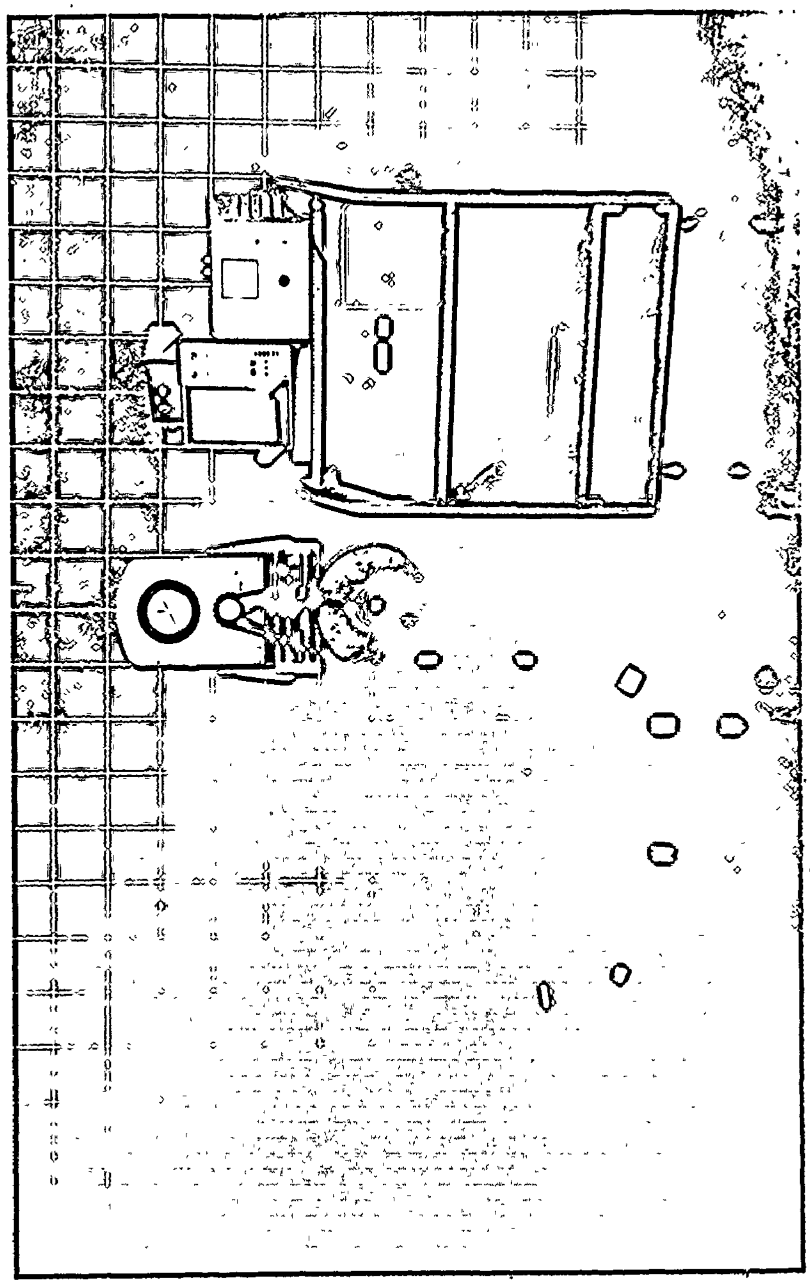


Figure 3. Gear and chain coupling system used to connect the Cybex II isokinetic dynamometer to the leg press training machine.

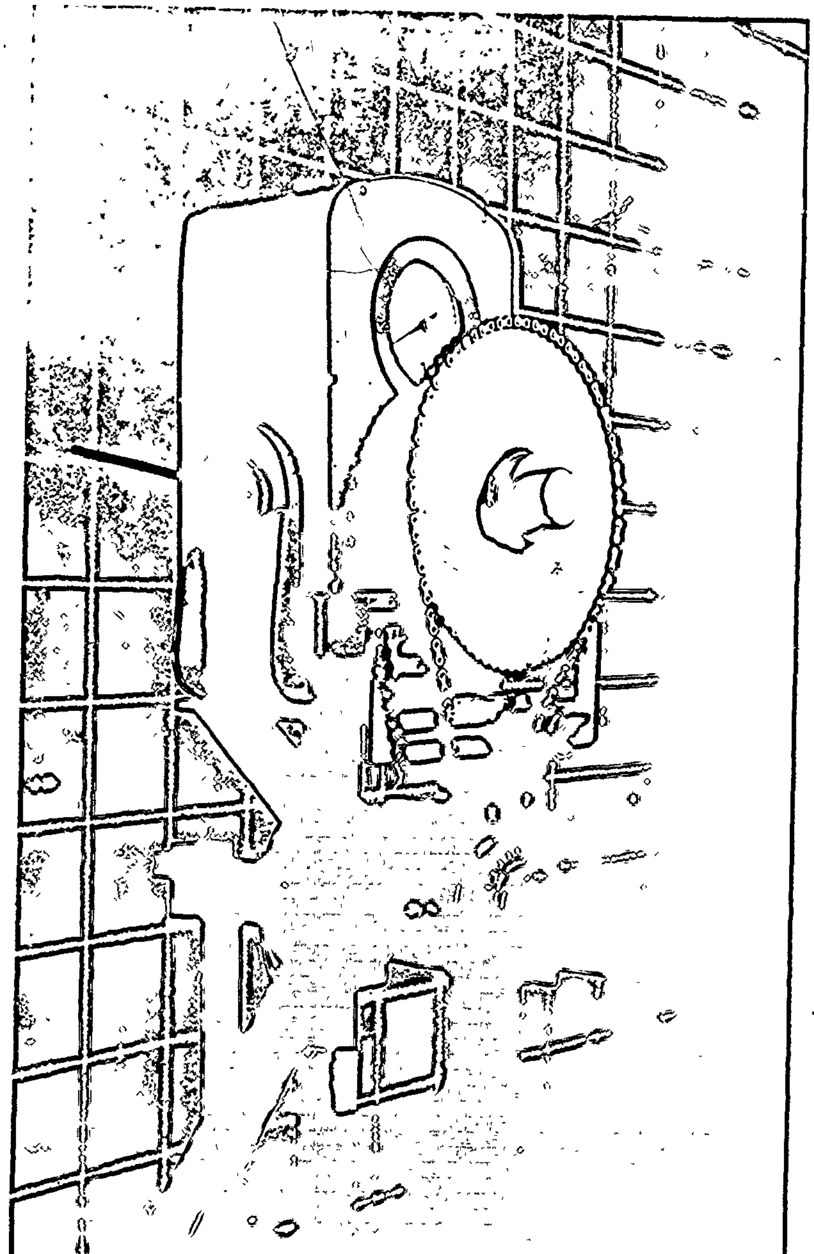
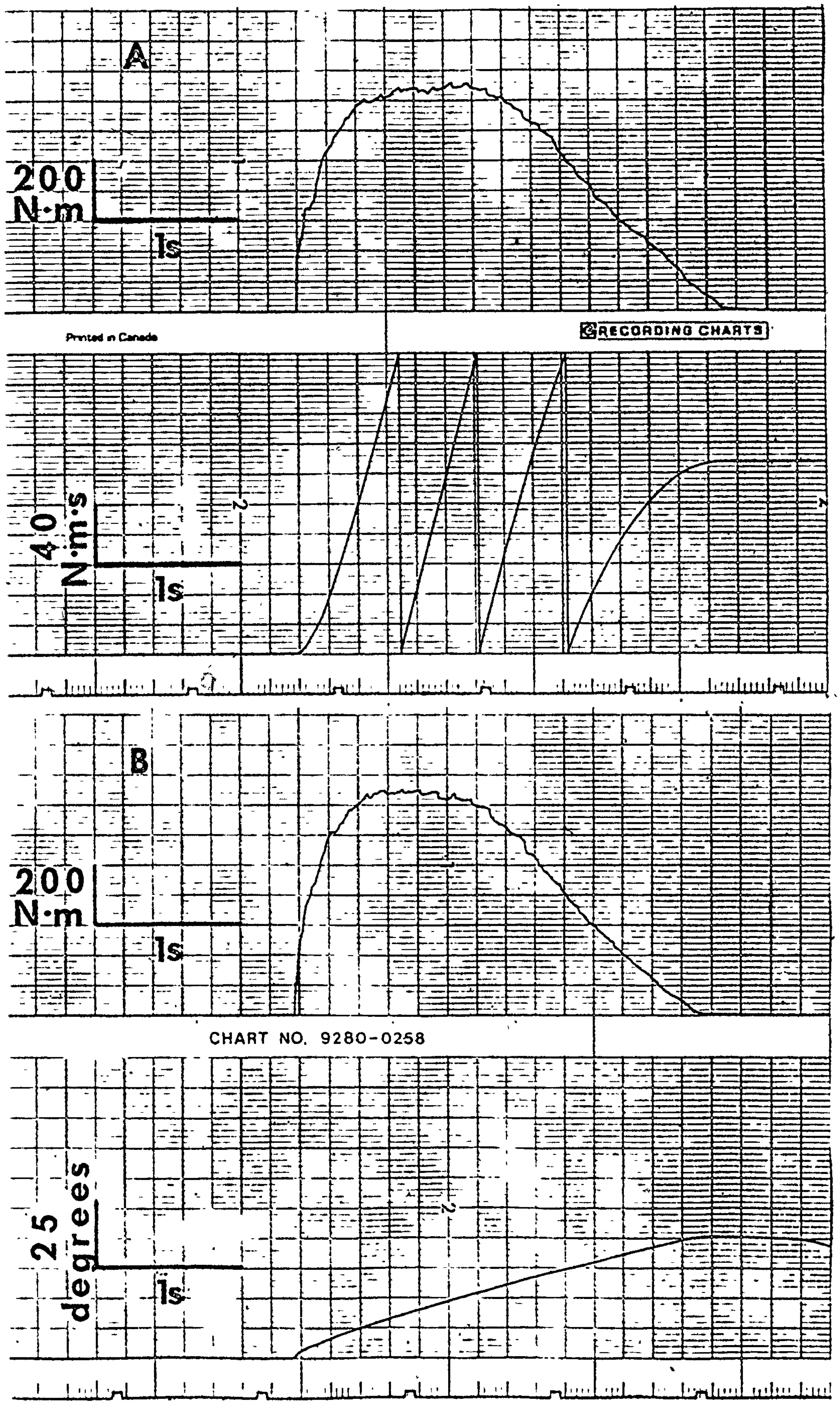


Figure 4. Recording of a maximal voluntary concentric leg press contraction at a velocity of 15°/s. A. The torque record is shown above a record of the integration of torque and time. B. The torque record is shown above the potentiometer record of the movement of the lever arm.


A
200
N·m
1s
Printed in Canada
RECORDING CHARTS
40
N·m·s
1s
B
200
N·m
1s
CHART NO. 9280-0258
25
degrees
1s

integration of torque and time and permitted the measurement of impulse in newton-metre-seconds (N.m.s), and average torque, measured as the impulse divided by the time of the contraction. Values for peak torque, average torque and impulse can be converted to peak power (W, watts), average power (W) and work (J, joules), respectively, by multiplying by the lever arm velocity (in rad/s, rad = radians, 1 radian = 57.3°/s.

The output from the potentiometer measuring the movement of the lever arm could also be displayed on Channel 2 of the recorder. An example of a typical record is given in Figure 4B. The angular velocity of the lever arm during the time of torque registration could be determined from this record, thus allowing for a comparison of the preset velocity with the actual measured contraction velocity. The length of the lever arm was 37.8 centimetres (cm) from the axis of rotation to the point of attachment of the footplate.

2. Strength-Velocity Relation

(a) Measurement of Maximal Voluntary Strength. The maximal voluntary strength of muscular contractions of the left, right and both limbs acting together in the leg press movement was measured at selected velocities from 0°/s to 424°/s. The order of velocities and the order of limbs tested was randomized across subjects. Subjects were given 3 warm-up contractions, followed by 3 test contractions for each type of contraction (left, right or bilateral) at each velocity tested. The highest value measured in the test contractions was reported in the results. Subjects were allowed to rest between test contractions for 20 seconds and also received intermittent longer rest periords when the apparatus was being altered for different velocities. Subjects were encouraged to give a maximal effort throughout the complete range of motion of each contraction.

The leg press movement consisted of extension of the leg from a starting position of 90 degrees of knee joint extension, which was determined with a goniometer, to full extension. Subjects were firmly strapped into the seat with a restraining belt across the hips. They also gripped stabilizer handles located on either side of the seat. Subjects were attached to the leg press lever arm by means of foot plates into which the feet were firmly secured with velcro straps.

Isometric testing was done with the knee joint angle at 100 degrees of extension, as determined with a goniometer. This knee joint angle was chosen because it was similar to that used by Secher et al. (1978), but also at a joint position that was extended from the starting position for dynamic contractions, thereby allowing for comparisons between the isometric and slow dynamic contractions at similar knee joint angles. Subjects were instructed to exert their maximal force against the fixed lever arm for 5 seconds.

The dynamic test velocities used in the leg press, according to the preset Cybex dial setting and gear ratios in use were 15°/s, 30°/s, 52.5°/s, 105°/s, 210°/s, 300°/s, 360°/s and 420°/s. However, measurement of the angular velocity of the lever arm with the use of the lever arm movement potentiometer showed the following results:

(1) The velocities of 15°/s, 30°/s and 52.5°/s corresponded equally between the 2 methods of measurement.

(2) At the velocity setting of 105°/s, for 3 subjects the bilateral velocity of contraction was greater than 105°/s, according to the potentiometer measurement. These subjects' values were not included in the results.

(3) At the velocity setting of 210°/s, the bilateral velocity of contraction was greater than the unilateral values for all subjects, according to the potentiometer method of measurement. No summed unilateral to bilateral comparisons were done. The velocity of contraction was found to be a mean of 216±0.6 (SE)°/s and 234°/s±2.1°/s for the unilateral and bilateral contractions respectively and these values were used in reporting the results.

(4) At the velocity settings of 300°/s, 360°/s and 420°/s, the velocity of the lever arm was found to be greater than the pre-set values in the unilateral and bilateral contractions, based on the potentiometer method of measurement. The measured velocities were similar between the unilateral and bilateral contractions and hence summed unilateral to bilateral comparisons were made. The velocity values were determined to be 332±2.3°/s, 380±2.1°/s and 424±0.6°/s for the 3 velocity settings of 300°/s, 360°/s and 400°/s, respectively.

In order to compare the maximal velocity of movement of unilateral and bilateral contractions, subjects were instructed to extend through the leg press movement as quickly as possible, starting from 90 degrees of knee extension. The lever arm was free to rotate, having been uncoupled from the Cybex II dynamometer. Subjects were given 3 practice trials and 3 test trials, of which the highest was reported. The maximal average velocity through 10 to 90% of the range of motion was calculated from the potentiometer record of the lever arm movement.

(b) Bilateral to Summed Unilateral Strength Ratio. Comparisons between the bilateral and unilateral muscular contractions were made by summing the strength values of the left and right legs tested separately, or unilaterally, to obtain a summed unilateral value and expressing this value relative to the strength of the 2 legs acting together, or bilaterally. In this manner, a bilateral to summed unilateral ratio or B/U ratio could be computed.

(c) Position at Time of Peak Torque. The amount of lever arm movement from the start of the contraction until the registration of peak torque was measured by comparing the torque record and record of lever arm movement. It was reported by Thorstensson et al. (1976) and Scudder (1980) that the peak torque in a knee extension movement was produced later in the arc of motion as the velocity of contraction was increased. This phenomenon was investigated in the present study for a leg press movement.

3. Fatigability. The fatigability of bilateral and unilateral muscular contraction was measured in a fatigue test consisting of 100 maximal voluntary contractions at a velocity of 105°/s. The velocity of 105°/s was chosen so that contractions would last approximately 0.5 seconds, which was similar to that reported in the literature for knee extension fatigue studies (Thorstensson, 1976; Nilsson et al., 1977; Tesch et al., 1978; Komi and Tesch, 1979). The movement used in the fatigue protocol was the same as that used in the strength velocity study. After each extension contraction, subjects were instructed

to return the lever arm to the starting position, with only the force necessary to bring it back at a velocity which was just less than the pre-set isokinetic velocity. Subjects were given adequate practice before the beginning of the fatigue test to familiarize themselves with the movements required. The strength of contractions was measured at the following stages of the fatigue test: initial, 10th, 25th, 50th, 75th and final contraction. These strength values were calculated in the following manner. The average of the peak torques of the best three out of the first six contractions was taken as the initial value. In a similar manner, the average of the best three out of the final six contractions was taken as the final value. This was done to avoid spuriously high or low values (Thorstensson, 1976). For the other stages, the average of the peak torques of the 9-11th, 24-26th, 49-51st and 74-76th were used to calculate the 10th, 25th, 50th and 75th values respectively. Endurance ratios at each stage of the fatigue test were computed by dividing the initial value into the appropriate other values. Subjects were encouraged to make maximal efforts throughout the one hundred contractions of the test.

4. Subjects. Subjects for the strength-velocity and fatigue studies were male physical education students who volunteered to participate after being informed of the nature of the study. None of the subjects was engaging in a regular weight training program at the time of the study. The characteristics of the 9 subjects who participated in the study were as follows: $\bar{X}$ age = 20.9 ± 0.97 years (SD), range = 20-23 years, $\bar{X}$ height = 173.8 ± 3.38 centimeters, range = 168.9-179.1 cm, $\bar{X}$ weight = 70.8 ± 3.32 kilograms, range = 64.3-74.6 Kg.

5. Reproducibility Study. The following measurements were repeated on 2 separate days on 8 subjects.

(1) Peak torque, average torque and impulse of right, left and bilateral contractions at 15°/s and 380°/s velocity on the leg press.

(2) Measurement of maximal average velocity through 10 to 90% of the range of motion for left, right and bilateral movements.

(3) The bilateral fatigue test.

As well, a study was made of the reproducibility of the peak torque generated in a contraction over repeated trials by comparing the 2 best trials at each velocity. This was also done for average torque and impulse values at the velocities of 15°/s and 380°/s on the leg press.

C. Statistical Methods

The descriptive statistics used in this study included the mean ($\bar{X}$), standard deviation (SD), standard error of the mean (SE), range (min-max) and the number of cases (N).

Correlations between pairs of variables in the EMG study were computed by the Pearson product-moment method (r).

Comparisons between different types of contractions, unilateral and bilateral, across velocities or stages of the fatigue test were examined with a two-factor repeated measures ANOVA. Prior to statistical analysis the data was transformed to equalize the variance across the velocities or fatigue stages. A probability level of $p < .05$ was considered significant.

The reproducibility of a measurement was determined by computing the "method error" (ME) statistic as used by Thorstensson et al.

(1976, 1977); Friman (1977) and Sale (1979). For measurements made twice on a group of subjects the ME was calculated using the formula:

$$ME = \sqrt{\sum (d-\bar{d})^2/2n-1}$$

in which d = the difference between the 2 measurements made on each subject, $\bar{d}$ = the mean difference and n = the number of subjects. The method error has been defined as the standard deviation for a single experiment (Thorstensson, 1976) and may be expressed in the units of measurement or as a coefficient of variation by using the following formula:

$$ME(V) = \frac{ME}{(\bar{X}_1+\bar{X}_2)/2} \times 100$$

in which ME(V) = the method error, expressed as a coefficient of variation, ME = the method error, $\bar{X}_1$ = the mean result of the group of subjects on the first testing occasion and $\bar{X}_2$ = the mean result on the second testing occasion. The coefficient of variation form was used in this study.

III. RESULTS

A. <u>Leg Press Electromyography</u>. Comparisons of the integrated, rectified electrical activity, recorded from surface electrodes placed on the right leg, during right only vs bilateral contractions at 0°/s, 15°/s and 380°/s test velocity settings are given in Tables 1, 2 and 3, respectively. It can be seen that the electrical activity recorded from the right leg was greater during right only contractions in most of the comparisons made at the 3 velocities. Examples of EMG recordings at the velocity settings of 0°/s, 15°/s and 380°/s are given in Figures 5, 6 and 7 respectively. When the muscles were compared within subjects, the highest ratios of EMG activity were found in the rectus femoris muscle at each velocity, while the vastus medialis and vastus lateralis tended to show similar ratios of electrical activity.

A summary table of the EMG results, which were pooled for each type of contraction is given in Table 4. A two factor repeated measures ANOVA revealed significant main effects of type of contraction (right only vs. bilateral) and velocity on integrated EMG activity. The interaction between these two variables was not significant. (See Appendix for ANOVA table.)

The mean ratio of the peak torques registered during right leg only contractions, to one-half of those registered during bilateral contractions, was 1.178 ± 0.112 (SE) under isometric conditions, 1.329 ± 0.031 at 15°/s velocity and 1.867 ± 0.077 at 380°/s. As shown in Figure 8, no significant correlation was found between the ratio of peak torques

Table 1. EMG activity recorded from right leg quadriceps muscles during right only and bilateral isometric contractions.

Subject	Vastus Medialis			Vastus Lateralis			Rectus Femoris		
	Right Only	Bilateral	Ratio	Right Only	Bilateral	Ratio	Right Only	Bilateral	Ratio
J.F.	12.12[1]	11.42	1.062	11.80	10.01	1.179	10.88	9.16	1.187
M.H.	5.84	4.15	1.408	6.65	3.58	1.857	3.63	0.34	10.583
G.P.	5.61	6.55	0.857	3.45	4.24	0.814	1.28	1.45	0.887
L.Y.	16.19	8.97	1.804	9.53	6.22	1.532	5.06	2.03	2.497
$\bar{X}$	9.94	7.77	1.283	7.86	6.01	1.346	5.21	3.25	3.789
SE	2.57	1.56	0.208	1.81	1.45	0.255	2.04	2.00	2.292

[1] Arbitrary units

Table 2. EMG activity recorded from right leg quadriceps muscles during right only and bilateral contractions at 15°/s velocity.

Subject	Vastus Medialis			Vastus Lateralis			Rectus Femoris		
	Right Only	Bilateral	Ratio	Right Only	Bilateral	Ratio	Right Only	Bilateral	Ratio
J.F.	5.08[1]	4.29	1.184	4.21	3.46	1.217	2.60	1.14	2.281
M.H.	2.48	3.36	0.738	3.05	3.25	0.939	0.96	0.78	1.231
G.P.	2.97	3.32	0.895	2.46	2.28	1.079	1.06	0.76	1.395
L.Y.	7.32	4.41	1.660	4.60	2.80	1.643	2.02	0.99	2.040
$\bar{X}$	4.46	3.85	1.119	3.58	2.95	1.220	1.66	0.92	1.737
SE	1.11	0.29	0.203	0.50	0.26	0.152	0.39	0.09	0.252

[1] Arbitrary units

Table 3. EMG activity recorded from right leg quadriceps muscles during right only and bilateral contractions at 380 °/s velocity.

Subject	Vastus Medialis			Vastus Lateralis			Rectus Femoris		
	Right Only	Bilateral	Ratio	Right Only	Bilateral	Ratio	Right Only	Bilateral	Ratio
J.F.	0.80[1]	0.53	1.500	0.53	0.45	1.166	0.53	0.49	1.083
M.H.	0.47	0.43	1.089	0.56	0.47	1.206	0.32	0.20	1.618
G.P.	1.45	1.16	1.254	0.72	0.73	0.990	0.34	0.22	1.534
L.Y.	1.31	1.46	0.897	0.96	0.81	1.187	0.82	0.47	1.749
$\bar{X}$	1.01	0.90	1.185	0.69	0.62	1.137	0.50	0.35	1.496
SE	0.23	0.25	0.128	0.10	0.09	0.050	0.12	0.08	0.145

[1] Arbitrary units

Figure 5. Electromyographic recordings from 3 right quadriceps muscles during a right leg only (R.O., left side of figure) and a bilateral (B.L., right side of figure) isometric leg press. EMG traces are from the vastus medialis: upper trace; rectus femoris: middle trace and vastus lateralis muscles: lower trace in each condition. Solid line is the torque record.

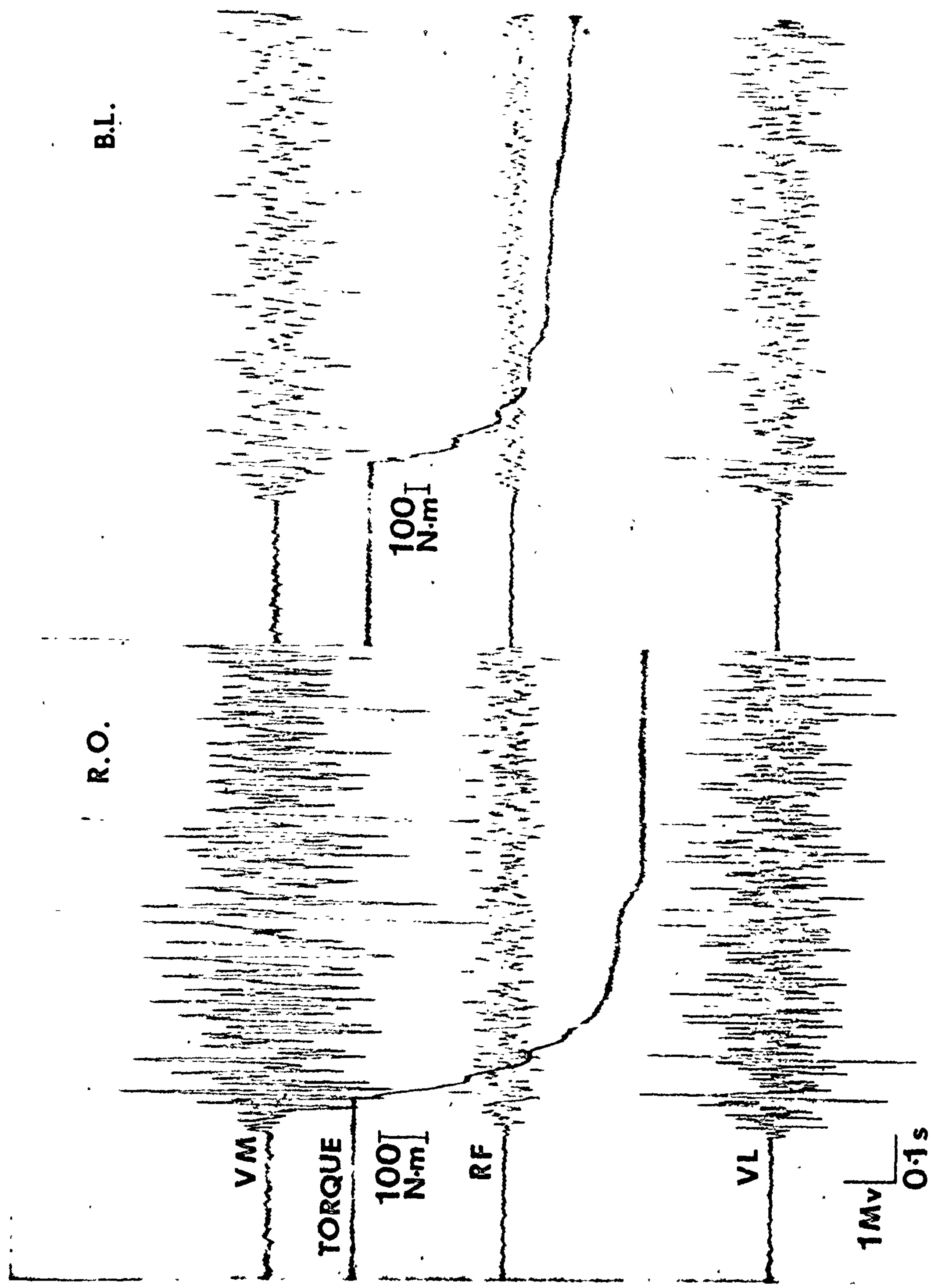
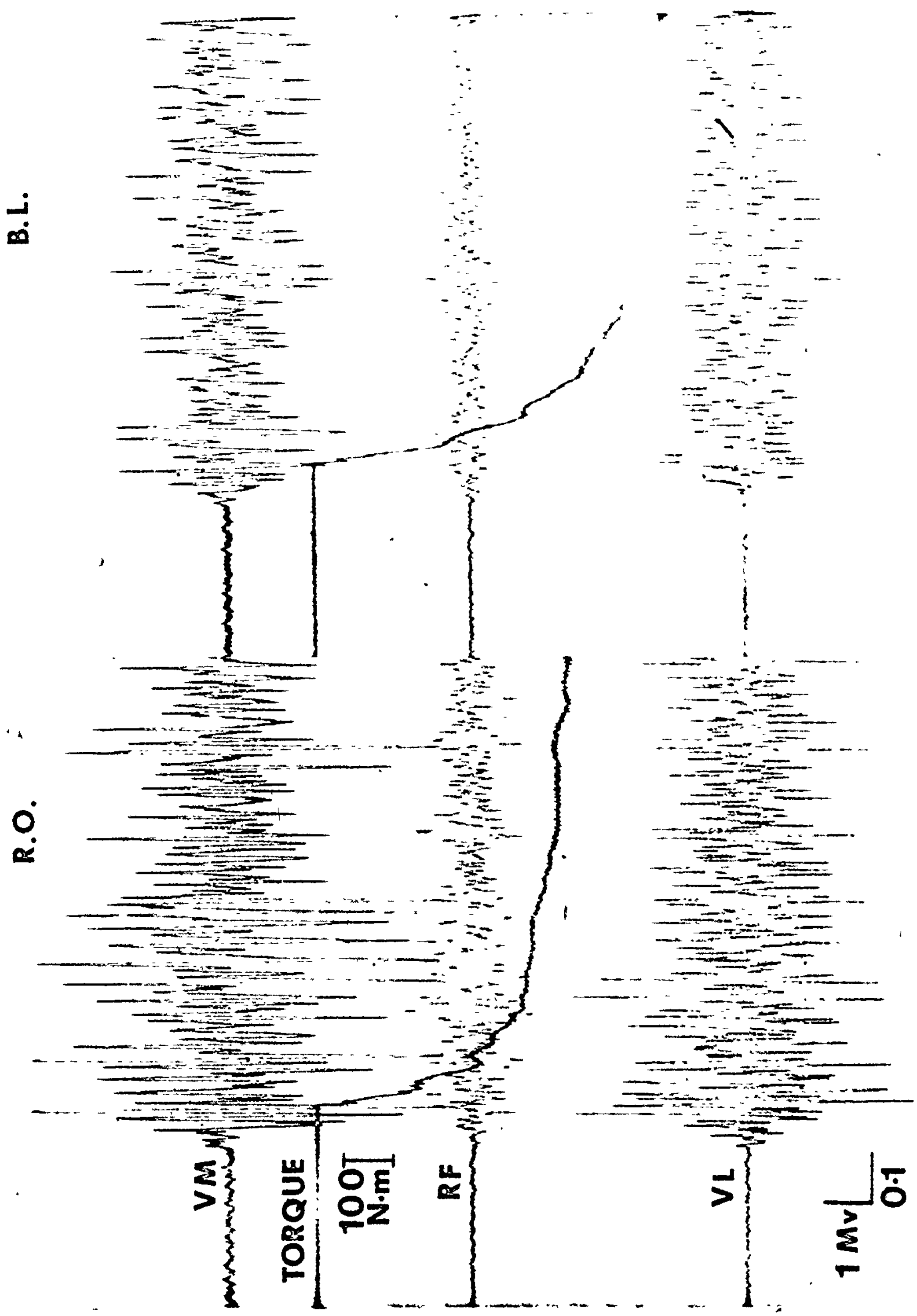

B.L.
R.O.
VM
TORQUE
100 N·m
100 N·m
RF
VL
1Mv
0·1s

Figure 6. Electromyographic recordings from 3 right quadriceps muscles during a right leg only (R.O., left side of figure) and a bilateral (B.L., right side of figure) leg press at a 15°/s velocity (angular velocity of the lever arm). EMG traces are from the vastus medialis: upper trace; rectus femoris: middle trace and vastus lateralis muscles: lower trace in each condition. Solid line is the torque record.



B.L.
R.O.
VM
TORQUE
100
N·m
RF
VL
1 Mv
0·1

Figure 7. Electromyographic recordings from 3 right quadriceps muscles during a right leg only (R.O., left side of figure) and a bilateral (B.L., right side of figure) leg press at a 380°/s velocity (angular velocity of the lever arm). EMG traces are from the vastus medialis: upper trace; rectus femoris: middle trace and vastus lateralis muscles: lower trace, in each condition. Solid line is the torque record.

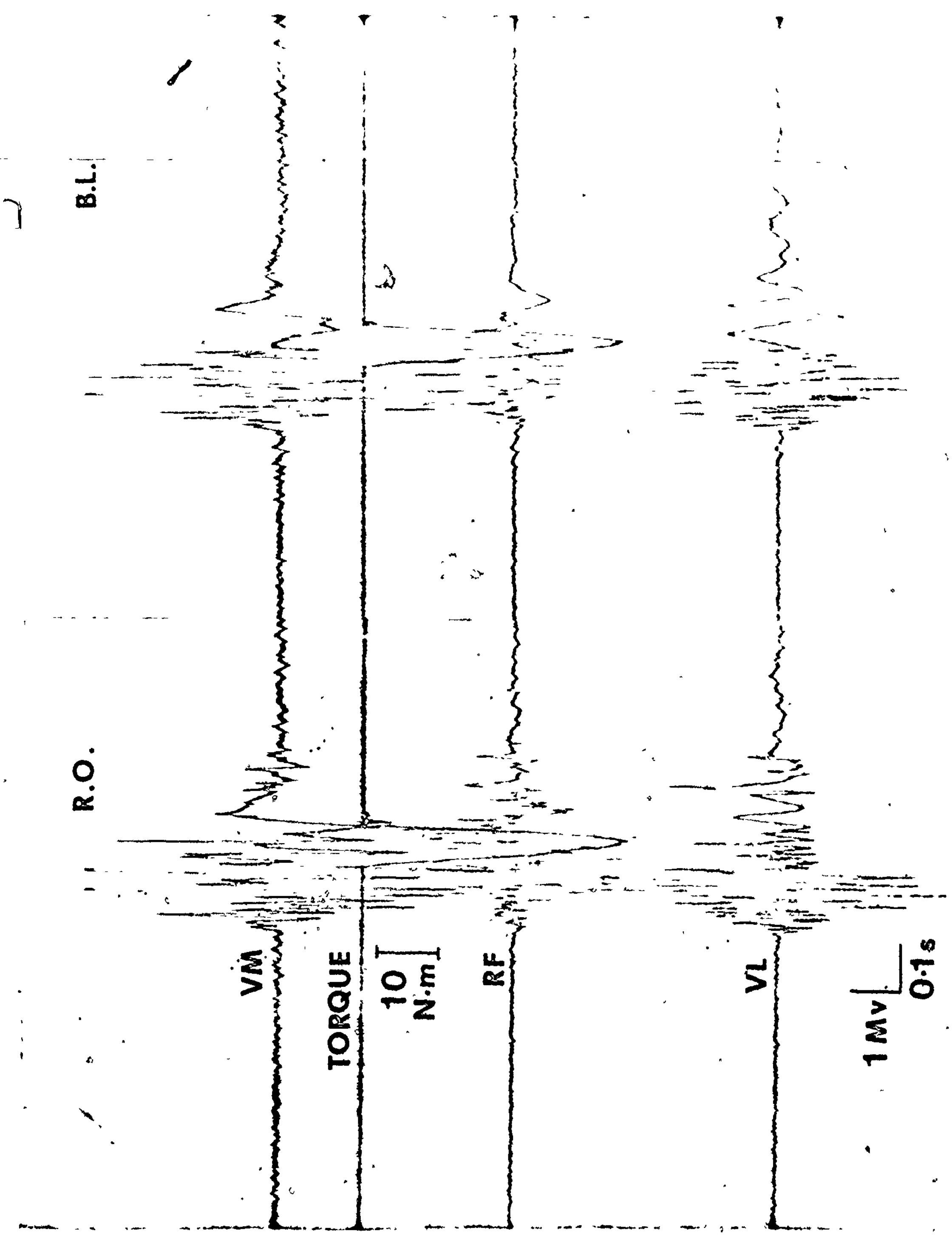

B.L.
R.O.
VM
TORQUE
10
N·m
RF
VL
1 Mv
0·1s

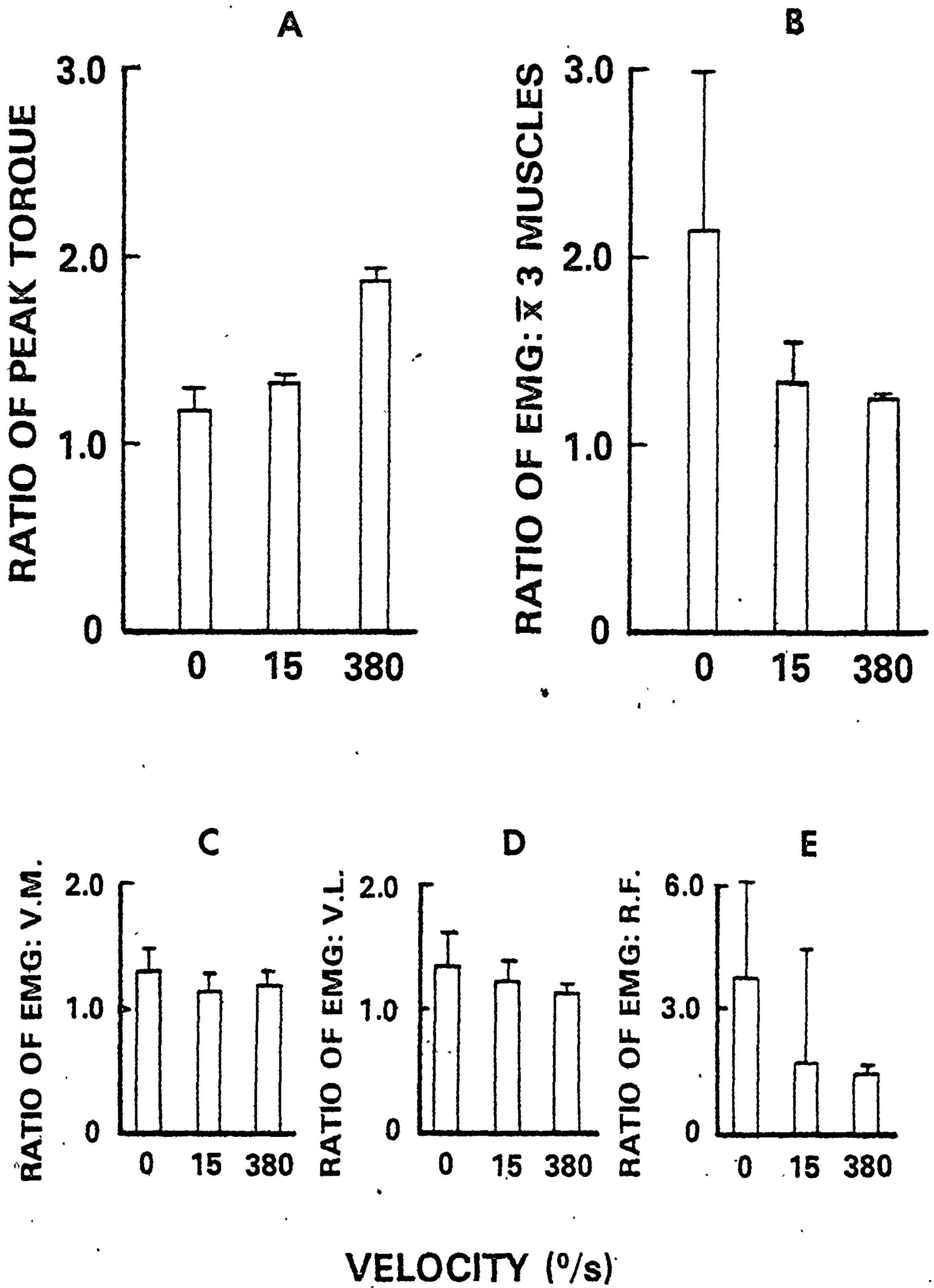
Table 4. Summary of EMG activity recorded from the right leg during isometric, 15 °/s and 380 °/s velocity right only and bilateral contractions.

Velocity (°/s)	Right Only	Bilateral	$\bar{X}$ Difference
0	7.67±1.27[1]	5.68±1.05	1.99±0.65
15	3.23±0.52	2.57±0.39	0.66±0.30
380	0.73±0.11	0.62±0.11	0.12±0..04

Values are $\bar{X}$ ± SE, N = 12

[1]Arbitrary units

Figure 8. Ratios of EMG activity and peak torque. Integrated EMG activities (IEMG) of three right quadriceps muscles (vastus medialis [V.M.], vastus lateralis [V.L.] and rectus femoris [R.F.]) were recorded during right only and bilateral leg extension contractions at 0°/s, 15°/s and 380°/s. The torque produced was also recorded. Ratios are of the values obtained in the right only (R.O.) condition over the values in the bilateral (B.L.) condition as follows: (A) Peak torque in R.O. over one-half of the peak torque in B.L. (B) Mean IEMG of the three muscles in R.O. over mean IEMG of three muscles in B.L. (C) IEMG of the V.M. in R.O. over IEMG of the V.M. in B.L. (D) and (E) same as for (C) except for the V.L. and R.F. muscles respectively. Values are $\bar{X}$ and SE, N=4. Velocity is the angular velocity of the lever arm.


A
B
RATIO OF PEAK TORQUE
RATIO OF EMG: x̄ 3 MUSCLES
3.0
2.0
1.0
0
0
15
380
C
D
E
RATIO OF EMG: V.M.
RATIO OF EMG: V.L.
RATIO OF EMG: R.F.
6.0
3.0
VELOCITY (°/s)

and the ratio of EMG activity for the individual muscles at the 3 velocities (vastus medialis, r = -0.020, vastus lateralis, r = -0.273, rectus femoris, r = -0.377), nor was there a correlation between the ratio of peak torques and the ratio of EMG activity averaged over the three muscles for each subject (r = -0.362).

It can also be seen in figure 8, that the mean ratio of EMG activity was highest in the rectus femoris muscle at each velocity, while the mean ratios of EMG activity in the vastus medialis muscle and vastus lateralis muscle were similar at each velocity. A particularly high ratio was found during isometric contractions in the rectus femoris muscle because in one subject (M.H.), the amount of EMG activity recorded during bilateral contractions was small, both in terms of the other subjects and relative to the right only condition.

B. Strength-Velocity Relation of Unilateral and Bilateral Muscular Contraction

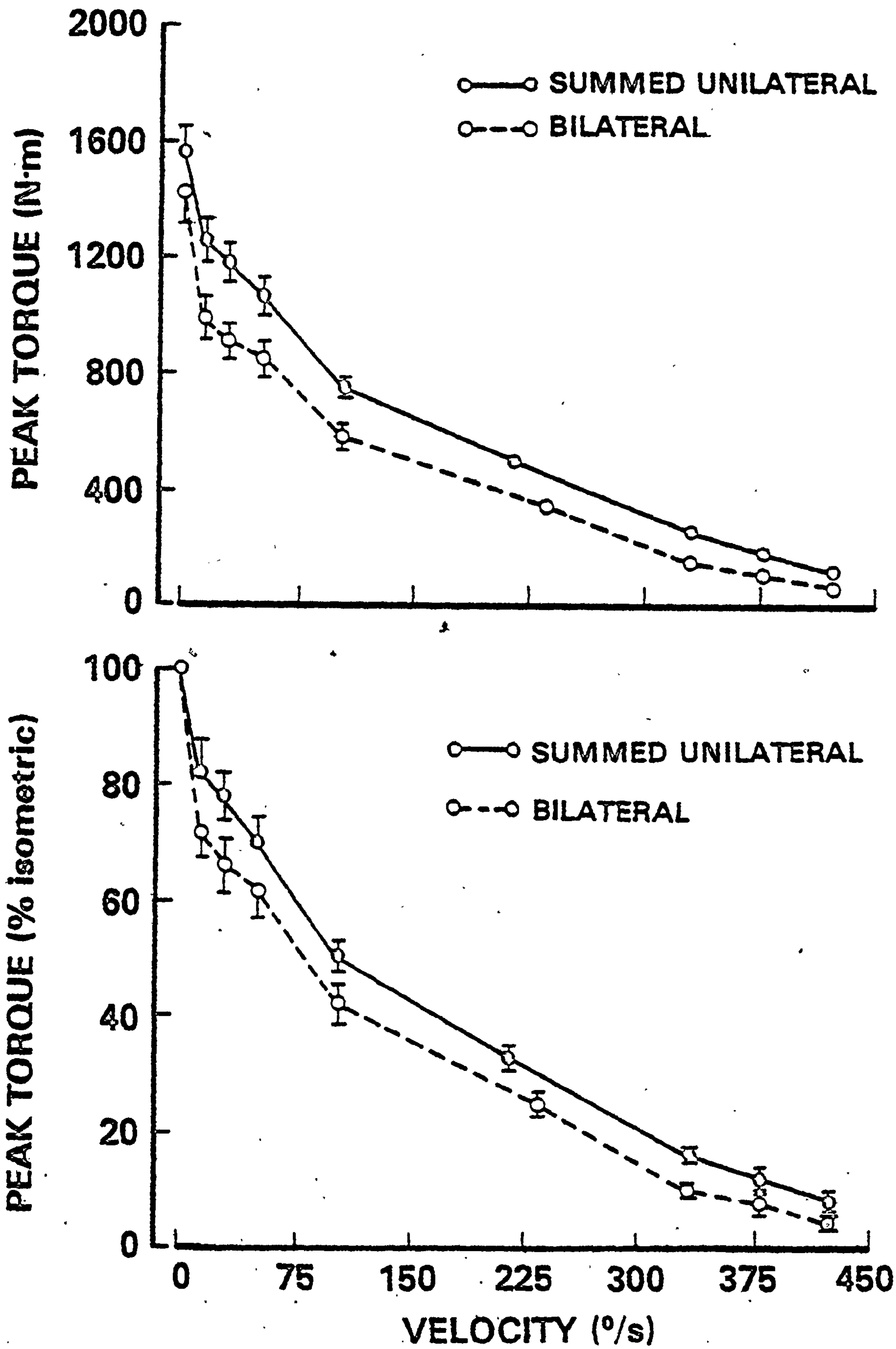
1. Peak Torque. The mean peak torque developed during bilateral contractions at selected velocities from 0 - 424 °/s is compared to the summed unilateral values in Table 5 and Figure 9. A two-factor repeated measures ANOVA revealed significant main effects of type of contraction (summed unilateral vs. bilateral) and velocity on peak torque. This was accompanied by a significant interaction between these two variables (See Appendix for ANOVA table). Pairwise comparisons of the summed unilateral and bilateral means were made at each velocity. All differences were found to be significant, indicating a greater development of peak torque in the summed unilateral condition.

Table 5. Comparison of leg press summed unilateral vs. bilateral peak torque.

Velocity (°/s)	Summed Unilateral (N.m)	Bilateral (N.m)	Difference (N.m)	B/U Ratio
0	1547.8±95.5	1407.8±90.0	140.0±41.7	0.910±0.025
15	1251.1±72.6	984.4±74.1	266.7±36.5	0.784±0.027
30	1177.8±59.5	906.7±53.8	271.1±30.6	0.769±0.022
52.5	1063.9±60.1	845.6±59.1	218.3±32.4	0.793±0.029
105	752.5±32.0	580.0±34.6	172.5±32.9[a]	0.772±0.038
216/234	497.5±14.5	342.9±11.1	-	-
332	255.2±10.5	146.9±9.8	108.3±6.4[b]	0.574±0.026
380	197.8±17.7	110.8±14.0	87.0±8.7	0.553±0.035
424	131.9±18.4	66.2±9.9	65.7±10.4	0.512±0.035

Values are $\bar{X} \pm$ SE, N = 9, except [a]N = 6, [b]N = 8.

Figure 9. Peak torque of summed unilateral and bilateral leg press contractions. The peak torques in newton-metres are given in the upper figure. The relative declines from isometric values in the summed unilateral and bilateral peak torques are given in the lower figure. Values are $\bar{X} \pm SE$, N=9, except at 105°/s, N=6; 332°/s, N=8. Velocity ranged from 0°/s to 424°/s. Velocity is the angular velocity of the lever arm.


2000
1600
1200
800
400
0
PEAK TORQUE (N·m)
SUMMED UNILATERAL
BILATERAL
100
80
60
40
20
0
PEAK TORQUE (% isometric)
SUMMED UNILATERAL
BILATERAL
0
75
150
225
300
375
450
VELOCITY (°/s)

A comparison was then made of the relative decline from isometric values in the summed unilateral and bilateral types of contraction (Figure 9), which revealed a greater decline in the bilateral condition. The B/U peak torque ratio decreased from 0.910 under isometric conditions to 0.512 at the highest test velocity of 424 °/s (Table 5), indicating that the bilateral peak torque became proportionately smaller than the summed unilateral as the velocity of contraction was increased. This difference in the relative decline of peak torque was supported by the significant interaction between contraction type and velocity.

The reproducibility of measurements of peak torque made using the modified Cybex II isokinetic dynamometer was as follows. The overall method error for the measurement of peak torque made on 2 separate days was 12.4%. This was similar to the method error of 13.7% reported for the measurement of peak torque of a knee extension movement on a conventional Cybex apparatus by Thorstensson et al. (1976), and also similar to the method errors reported by other authors (Sale, 1979; Tesch, 1980). Tables of the method error of peak torque measurements made on separate days and also of measurements made on repeated consecutive trials at the same velocity, can be found in the Appendix. The overall method error for the measurement of the bilateral to summed unilateral ratio of peak torques made on 2 separate days was 8.4%. The reproducibility of the measurement of this variable has not been previously reported, but it appeared to be a consistent phenomenon that was reproducible over separate testing occasions. The method errors regarding the B/U ratio measurements are also included in the above Appendix tables. No significant differences were found between the peak torque or B/U ratio values obtained on the 2 separate testing occasions.

The relative peak power of summed unilateral and bilateral contractions over the range of test velocities is presented in Figure 10. These values, as they were derived directly from the peak torque values, have the same significant differences as in the comparison of relative decline in peak torque. The maximum power output was reached at the velocities of 216 °/s and 234 °/s for the summed unilateral and bilateral conditions respectively, after which the power output showed a decline.

2. Average Torque and Impulse. Comparisons of the mean summed unilateral to bilateral average torques and impulses produced at the seven concentric test velocities are given in Table 6 and Figure 11, and Table 7 and Figure 12, for the average torque and impulse measures respectively. A two-factor repeated measures ANOVA was applied to each measure, which revealed significant main effects of type of contraction (summed unilateral vs. bilateral) and velocity, accompanied by a significant interaction, in both the average torque and impulse data (See Appendix for ANOVA tables). Pairwise comparisons of summed unilateral and bilateral means were made at each velocity. All differences were significant, indicating greater average torque and impulse values in the summed unilateral type of contraction.

The relative decline in average torque and impulse values from the slowest velocity (15 °/s), as the velocity of concentric contraction was increased, was found to be greater in the bilateral

Figure 10. Relative peak power of summed unilateral and bilateral leg press contractions. Relative peak power was derived as the product of relative peak torque values and the velocity. Relative peak torque values are given in the upper figure, relative peak power values in the lower figure. Values are $\bar{X} \pm$ SE, N = 9, except at 105°/s, N = 6; 332°/s, N = 8. Velocity ranged from 0°/s to 424°/s. Velocity is the angular velocity of the lever arm.

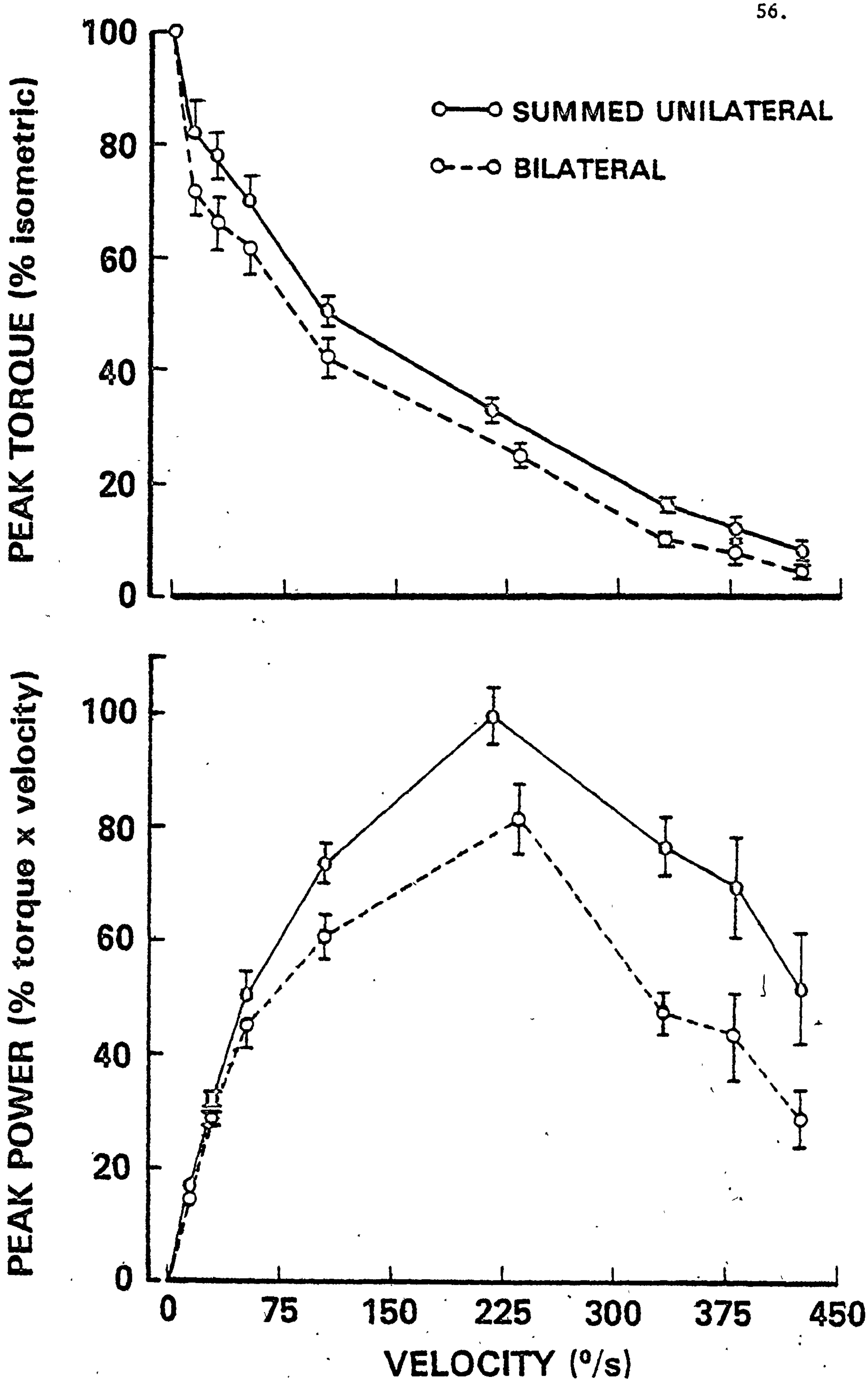

100
80
60
40
20
0
PEAK TORQUE (% isometric)
SUMMED UNILATERAL
BILATERAL
100
80
60
40
20
0
PEAK POWER (% torque x velocity)
0
75
150
225
300
375
450
VELOCITY (°/s)

Table 6. Comparison of leg press summed unilateral vs. bilateral average torque.

Velocity (°/s)	Summed Unilateral (N.m)	Bilateral (N.m)	Difference (N.m)	B/U Ratio
15	774.6±38.2	598.9±39.7	175.8±16.0	.769±0.023
30	724.8±36.6	560.3±31.0	164.5±20.2	.775±0.026
52.5	650.7±33.2	502.4±33.2	148.3±16.8	.770±0.025
105	473.6±21.1	345.9±19.6	127.7±21.6[a]	.734±0.037
216/234	270.7±12.9	183.3±5.2	-	-
332	141.9±4.1	81.4±6.3	60.5±4.6[b]	.571±0.037
380	106.3±11.7	62.9±9.1	43.4±4.8	.583±0.040
424	72.3±10.8	39.9±6.4	32.4±6.1	.559±0.045

Values are $\bar{X} \pm$ SE, N = 9 except [a]N = 6, [b]N = 8

Table 7. Comparison of leg press summed unilateral vs. bilateral impulse.

Velocity (°/s)	Summed Unilateral (N.m.s)	Bilateral (N.m.s)	Difference (N.m.s)	B/U Ratio
15	2174.3±197.5	1572.9±146.5	601.4±69.0	.723±0.018
30	1031.9±87.0	756.8±66.5	275.1±42.9	.736±0.033
52.5	555.8±46.1	413.4±37.6	142.4±16.9	.741±0.024
105	206.4±22.6	139.3±17.5	67.1±9.2[a]	.674±0.032
216/234	48.0±3.1	30.2±1.8	-	-
332	16.7±1.1	9.3±0.8	7.4±0.5[b]	.555±0.028
380	10.6±1.5	6.1±1.0	4.5±0.7	.575±0.048
424	6.2±1.2	3.1±0.5	3.1±0.8	.527±0.055

Values are $\bar{X}$ ± SE, N = 9, except [a]N = 6, [b]N = 8

Figure 11. Average torque of summed unilateral and bilateral leg press contractions. In the upper figure, the absolute values are shown and in the lower figure the relative decline in each condition from 15°/s values. Values are $\bar{X}$±SE, N=9 except at 105°/s, N=6, 332°/s, N=8. Velocity is the angular velocity of the lever arm.

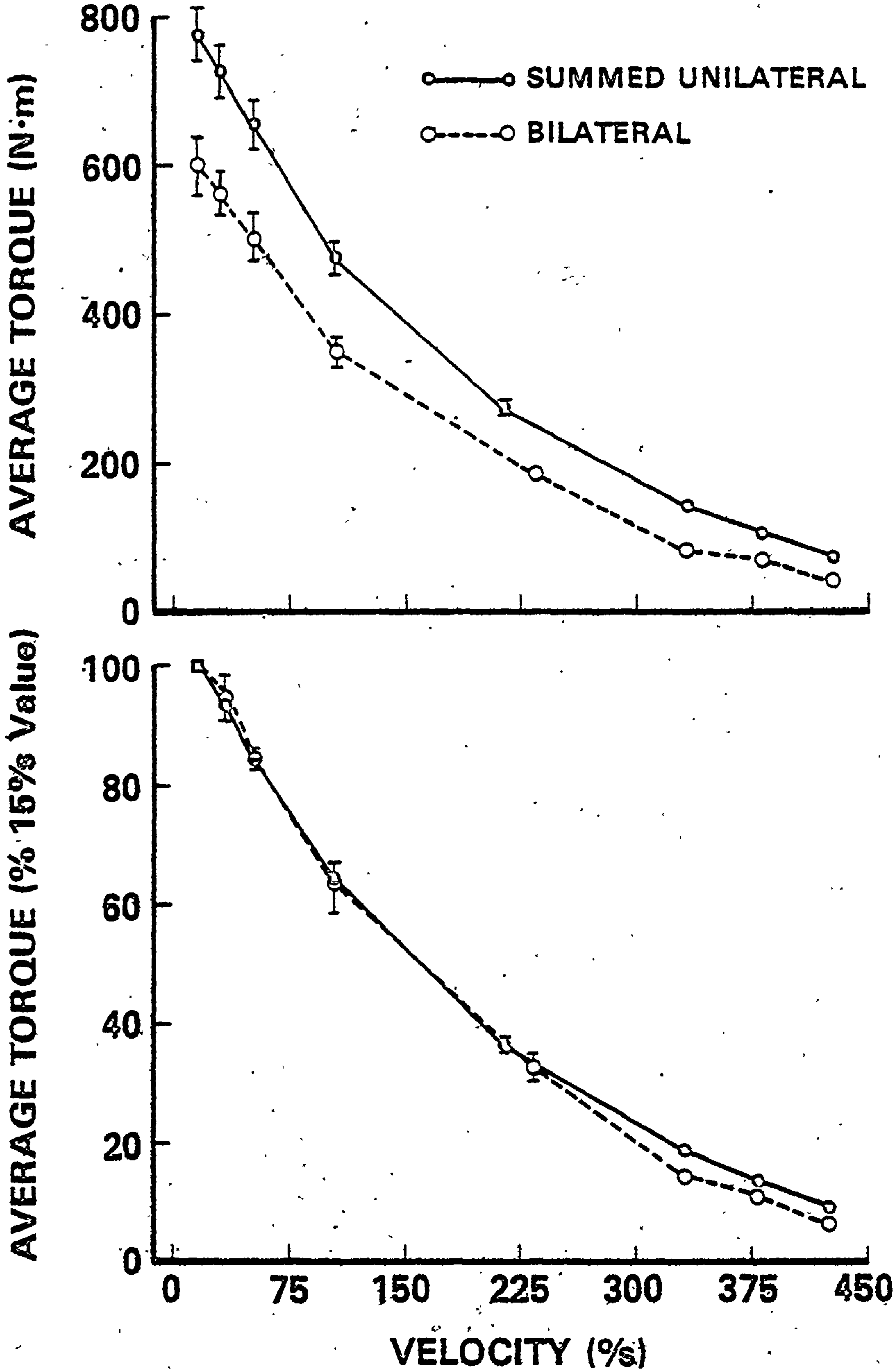
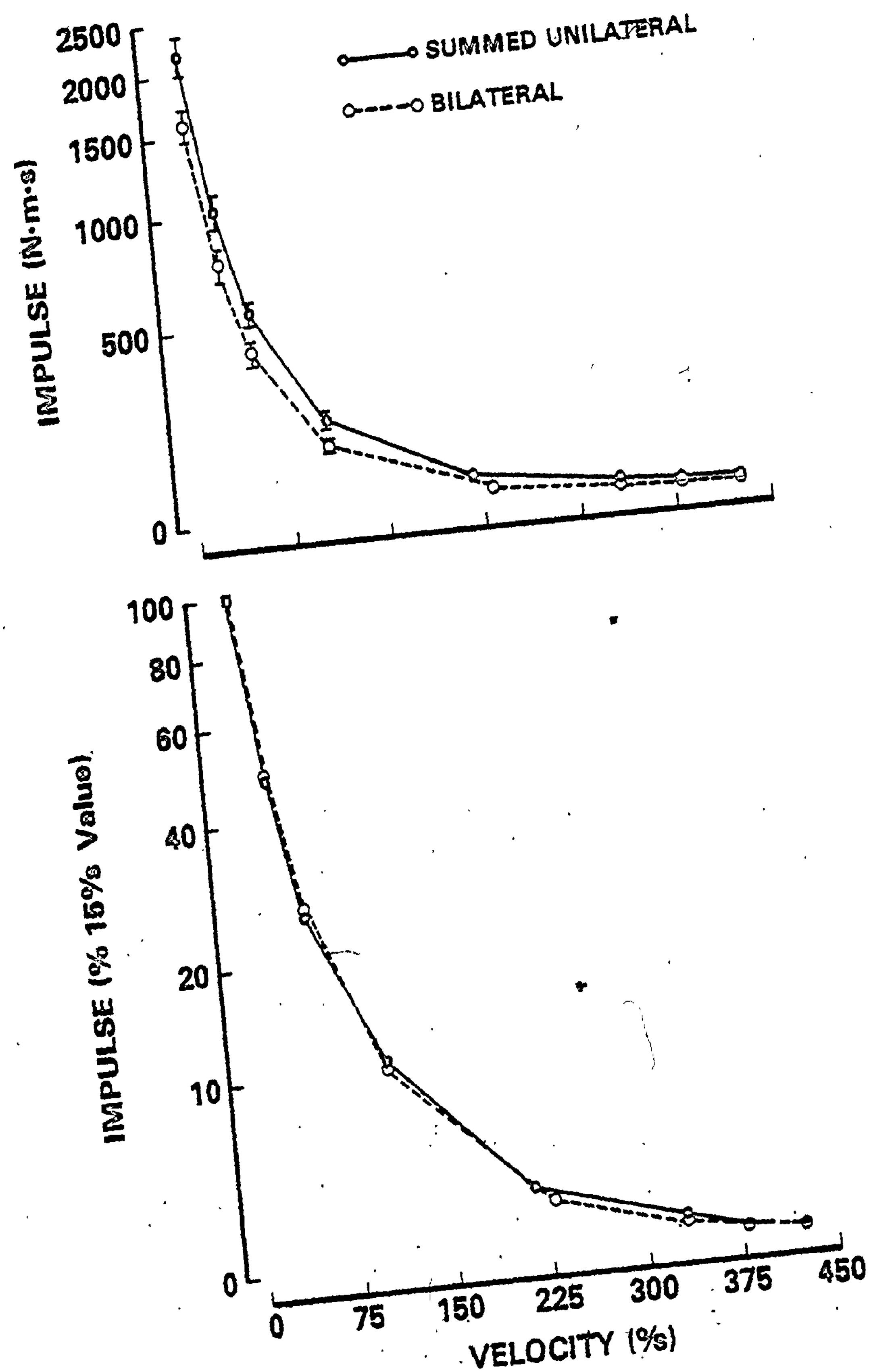

SUMMED UNILATERAL
BILATERAL
AVERAGE TORQUE (N·m)
800
600
400
200
0
AVERAGE TORQUE (% 15°/s Value)
100
80
60
40
20
0
0
75
150
225
300
375
450
VELOCITY (°/s)

Figure 12. Impulse of summed unilateral and bilateral leg press contractions. In the upper figure, absolute values are shown, and in the lower figure the relative decline in each condition from 15°/s values. Values are $\bar{X} \pm SE$, N=9, except at 105°/s, N=6, 332°/s, N=8. Velocity is the angular velocity of the lever arm.


SUMMED UNILATERAL
BILATERAL
IMPULSE (N·m·s)
2500
2000
1500
1000
500
0
IMPULSE (% 15°/s Value)
100
80
60
40
20
10
0
0
75
150
225
300
375
450
VELOCITY (°/s)

contractions, in the case of both measures (See Figures 12 and 13, average torque and impulse measures respectively). As supported by the significant interaction effect, the average torque and impulse B/U ratios changed with increasing velocity of contraction; the bilateral values becoming proportionately less than the summed unilateral values at high velocities. The overall similarity in the B/U ratios of the three measures of peak torque, average torque and impulse at the different concentric contraction velocities can be seen in Figure 13, in which they are presented together.

The overall method error for the measurement of average torque made on two separate days was 13.2%, and for impulse measurements was 17.0%. These method errors were higher than those reported by Sale (1979) for measurments made of knee extension strength on a conventional Cybex, but similar to those reported by the same author regarding ankle plantar flexion strength. The method errors for the measurement of the B/U ratios of average torque and impulse were 9.2% and 8.2% respectively. Tables of method errors for these measurements are also included in the Appendix. No significant differences were found between the values obtained on the two testing occasions.

3. Maximal Average Velocity. The maximal average velocity which subjects could achieve unilaterally and bilaterally, measured through 10 to 90% of the range of motion, is given in Table 8. It can be seen that both the right and left legs moving unilaterally were significantly faster than when both legs were contracting together. The method error for the measurement of this variable

Figure 13. B/U ratios for leg press peak torque, (left bar), average torque (middle bar) and impulse values (right bar) through a range of velocities. Values are $\bar{X}$ and SE, N=9, except at 105°/s, N=6; 332°/s, N=8. Velocity is the angular velocity of the lever arm.

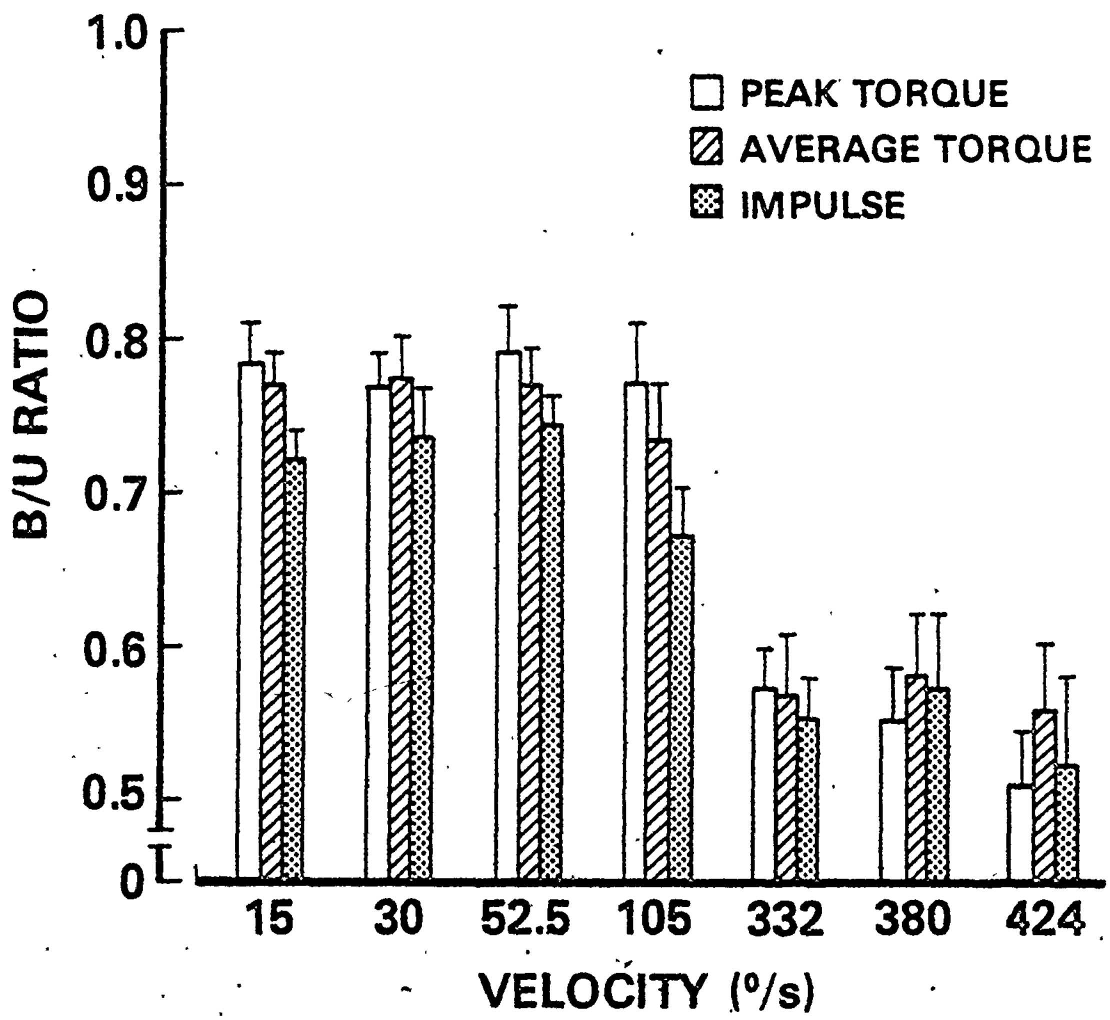

1.0
0.9
0.8
0.7
0.6
0.5
0
B/U RATIO
PEAK TORQUE
AVERAGE TORQUE
IMPULSE
15
30
52.5
105
332
380
424
VELOCITY (°/s)

Table 8. Maximal average velocity through 10 to 90% of the range of motion on the leg press.

Left (°/s)	Right (°/s)	Bilateral (°/s)	Difference		
			Left vs Right	Left vs Bilateral	Right vs Bilateral
488.8±11.3	503.4±12.7	472.7±11.7	-14.6±4.6*	16.1±6.4*	30.7±9.1**

Values are $\bar{X} \pm$ SE, N = 9

*p <.05, **p <.01

on two separate days was 5.0%, which was in close agreement with the day to day method error of 5.2% for the measurement of maximal knee extension velocity reported by Thorstensson (1976).

4. Position at Time of Peak Torque. A comparison of the position of the lever arm at the time of peak torque registration in unilateral and bilateral contractions is given in Table 9. The degrees of movement of the lever arm from the starting position to the position at the time of peak torque increased progressively as the velocity of contraction increased. The differences in the position of the lever arm at the time of peak torque registration between unilateral and bilateral contractions were small, non-significant and non-systematic. This comparison is illustrated in Figure 14. The mean total range of motion that subjects rotated the lever arm through during the leg press was 54.2 ± 3.70 (SD) degrees.

C. Fatigability of Unilateral and Bilateral Muscular Contraction

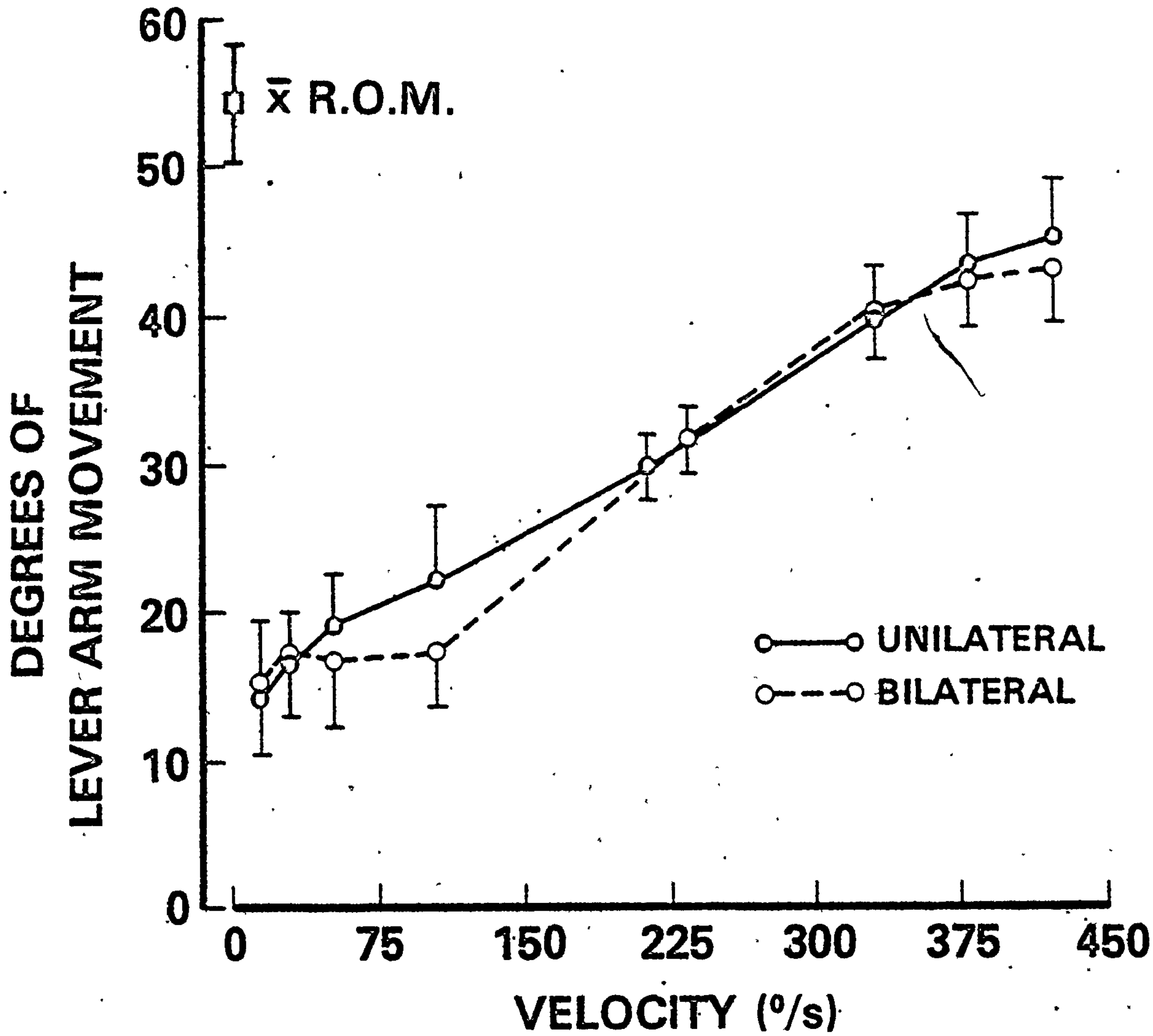
The mean peak torques of summed unilateral and bilateral contractions at selected stages of the fatigue test are shown in Table 10 and Figure 15. A two-factor repeated measures ANOVA revealed significant main effects of type of contraction (summed unilateral vs. bilateral) and stage of the fatigue test on peak torque. This was accompanied by a significant interaction between these two variables (See Appendix for ANOVA table). Pair-wise comparisons of the summed unilateral and bilateral means were made at each stage of the fatigue test. All differences were significant, indicating a greater development of peak torque in the summed unilateral

Table 9. Comparison of leg press unilateral vs bilateral position of lever arm at time of peak torque.

Velocity (°/s)	Degrees of Movement from Starting Position: Left and Right Combined	Bilateral	Difference
15	14.1±3.8	14.9±4.6	0.8
30	16.5±3.7	16.7±3.2	0.2
52.5	19.1±3.5	16.6±4.3	2.5
105	21.9±5.3[a]	17.1±3.6[a]	4.8
216/234	29.6±2.1	31.4±2.2	1.8
332	39.4±2.5[b]	39.9±3.0[b]	0.5
380	42.9±3.6	42.0±3.0	0.9
424	44.7±4.3	42.7±3.4	2.0

Values are $\bar{X} \pm$ SD, N = 9, except [a]N = 6, [b]N = 8

Figure 14. Position of the leg press lever arm at the time of peak torque registration. Unilateral values are compared to bilateral values. Values are $\bar{X} \pm SD$, N=9 subjects, except at 105°/s, N=6; 332°/s, N=8. Velocity is the angular velocity of the lever arm. $\bar{X}$ R.O.M. is the mean total range of motion. Included is ± one SD, N=9.



DEGREES OF LEVER ARM MOVEMENT
0
10
20
30
40
50
60
x̄ R.O.M.
UNILATERAL
BILATERAL
0
75
150
225
300
375
450
VELOCITY (°/s)

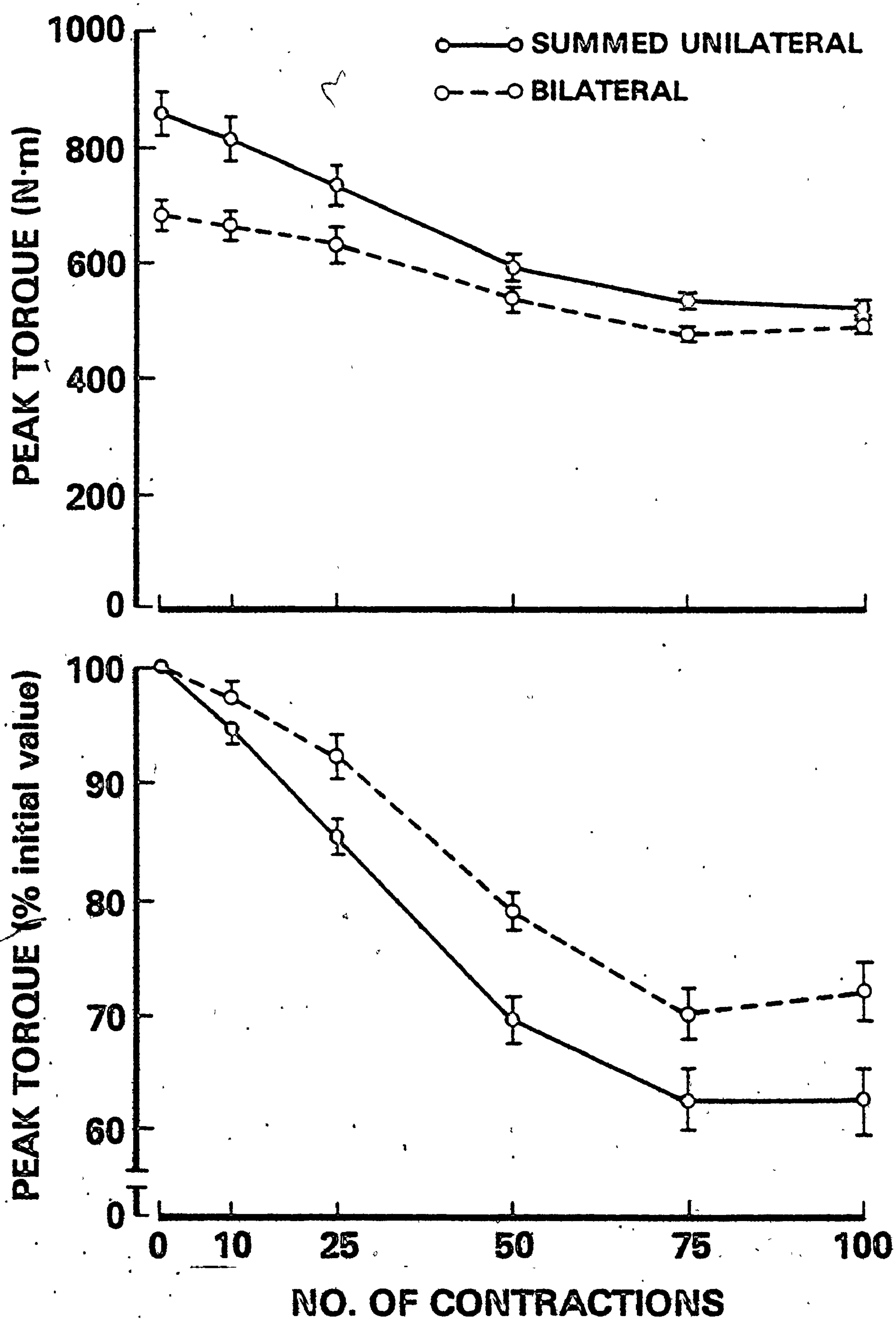
Table 10. Comparison of leg press summed unilateral vs bilateral fatigue.

No. of Contractions ($\bar{X}$ of)	Summed Unilateral Peak Torque (N.m)	Bilateral Peak Torque (N.m)	Difference (N.m)	B/U Ratio
1-6[1]	858.8±35.7	681.9±22.8	176.9±17.0	0.797±0.014
9-11	814.4±36.2	663.5±24.6	150.9±16.9	0.818±0.015
24-26	733.3±34.8	628.4±24.6	104.9±18.5	0.862±0.021
49-51	593.4±21.5	540.2±18.8	53.2±13.0	0.912±0.020
74-76	533.7±18.3	476.5±15.4	57.2±12.1	0.900±0.020
95-100[1]	525.8±14.7	489.5±17.2	36.4±11.3	0.931±0.020

Values are $\bar{X} \pm$ SE, N = 9

[1]Best 3 out of 6 were measured.

Figure 15. Comparison of fatigue in the summed unilateral and bilateral leg press contractions. A. The peak torque in the 2 conditions is shown. B. The relative decline from initial values in summed unilateral and bilateral conditions over the 100 fatiguing contractions is shown. Values are $\bar{X} \pm SE$, N=9.


SUMMED UNILATERAL
BILATERAL
1000
800
600
400
200
0
PEAK TORQUE (N·m)
100
90
80
70
60
0
PEAK TORQUE (% initial value)
0
10
25
50
75
100
NO. OF CONTRACTIONS

condition, at each stage of the test.

A comparison was then made of the relative decline from initial values that occurred in the two types of contraction over the course of the fatigue test (Figure 15). At the end of the test, the mean decline in peak torque in the summed unilateral condition was to 62.4% of initial values, and the bilateral value was 72.2%, indicating lesser fatigue in the bilateral type of contraction. This difference in relative decline was supported by the significant interaction effect found in the ANOVA. After ten contractions in the fatigue test, the mean summed unilateral decline was to 94.7% of initial values, while the bilateral value was 97.2%. At this stage, there had been only slight fatigue in the bilateral condition.

The method error for the measurement of the decline in peak torque in the bilateral fatigue test, made on two separate days was 6.8% for measurements made at the fifty contraction stage of the test and 6.6% for measurements made after the full one hundred contractions of the test. These method errors were of comparable size to the method error of 3.2% reported by Thorstensson (1976), and 6.9% reported by Tesch (1980), for day to day method errors in a fifty and one hundred contraction knee extension fatigue test, respectively.

IV. DISCUSSION

A. Motor Unit Activation in Unilateral and Bilateral Muscular Contraction

There appeared to be a greater motor unit activation in the quadriceps muscles in unilateral muscular contractions as compared to bilateral contractions, based on the electrophysiological evidence collected. Significantly more integrated EMG was recorded from three of the right quadriceps muscles: vastus medialis, vastus lateralis and rectus femoris, during right leg presses as compared to bilateral leg presses, done isometrically, and at a low and high velocity. This effect was observed in all three of the above muscles at each velocity, although it was not shown consistently by all subjects in all three muscles. The variability observed between subjects in the pattern of activation of the three muscles in the leg press movement was consistent however with previous reports of variation between individuals in the activation pattern of the different heads of the quadriceps femoris muscle in knee extension (Basmajian _et al_., 1972; Eloranta and Komi, 1980).

The greater integrated EMG activity recorded from the quadriceps muscles during a unilateral contraction was taken to represent a greater tension development in those muscles (Bigland and Lippold, 1954; Gans and Noordergraff, 1975; Milner-Brown and Stein, 1975; Kimura, 1977; Pollack, 1980). The relative contributions of an increased firing frequency and an increased motor unit recruitment to the increased EMG activity cannot be delineated in this type of recording, but normally both might be expected to have some influence (Person and Kudina, 1972). One possible assumption is that there was the same pattern of orderly recruitment of motor units in each type of contraction, unilateral and bilateral (based on the work of Milner-Brown et al. [1973a] and Desmedt and Godaux [1977, 1979]). It would then follow that the same units that were recruited in bilateral contractions were also recruited in the unilateral condition. Additionally, there was an increased firing frequency in these common units and/or a recruitment of more motor units in the unilateral efforts.

It was observed that although the ratio of peak torques of the right unilateral muscular contraction to bilateral contractions increased as the velocity of contraction was increased from 0°/s to 15 and 380°/s, the ratio of EMG activity did not change in a similar fashion; rather, there was no correlation between the two variables. This finding suggested that the increase in the activation of the available motor units during unilateral contractions, as compared to bilateral, was similar at each of these velocities. Thus, the proportionately greater strength of unilateral contractions at concentric velocities appeared to be due to an enhanced capacity of those motor units undergoing more activation in the unilateral situation to generate tension during concentric contractions. This enhanced capacity is characteristic of FT motor units. Further data regarding the tentative hypothesis derived from this data, that FT motor units were being activated to a greater extent in unilateral contractions, is described below in the investigations that compared the strength-velocity relation and fatigability of unilateral and bilateral muscle contractions.

B. Strength-Velocity Relation and Fatigability of Unilateral and Bilateral Muscular Contraction

1. Strength-Velocity Relationship

(a) Isometric comparison of unilateral and bilateral strength. The mean summed unilateral isometric peak torque was found to be significantly greater than the bilateral isometric value in this part of the study in which the left only, right only and bilateral strength was measured; the resultant B/U ratio was 0.910. This ratio was higher than the ratio of 0.75 reported by Secher et al. (1978), but Secher (1975) has presented evidence that the B/U strength ratio can vary between subject groups, possibly as a result of different levels of strength training. Other investigators have also reported B/U strength ratios of less than unity: Secher et al. (1976); Rube et al. (1979) and as reported in Secher et al. (1978): Asmussen et al. (1959) and Asmussen and Heeboll-Nielsen (1961). The greater summed unilateral isometric strength was taken as evidence of increased motor unit activation in unilateral muscular contraction, as described above.

(b) Decline in strength with increasing velocity. A lesser decline in the peak torque of summed unilateral contractions, relative to isometric values, was observed when compared to the decline in bilateral contractions. Thorstensson et al. (1976, 1977); Coyle et al. (1979) and Gregor et al. (1979) all reported a lesser decline in single leg knee extension peak torque with increasing velocity of contraction in subjects with a higher proportion of FT muscle fibre in their vastus lateralis muscle. Thus, it appears that there may have been a greater proportion of FT motor units active in the unilateral muscular contraction as compared to bilateral.

This conclusion is consistent with the generally held view that the fast-twitch motor unit is functionally adapted to produce greater tension than the slow-twitch motor unit when rapid force development in dynamic muscular contraction is required, due to its faster twitch contraction time (for review of motor unit differences see Burke and Edgerton, 1975 and also Gydikov et al., 1976). Vittasalo and Komi (1978) have reported that the time of tension development in a leg press movement was positively correlated with the % ST muscles fibres in the vastus lateralis, thereby suggesting that those subjects with higher proportions of FT fibres had faster rates of rise of tension development.

The decline in peak torque registered by the contracting muscles over increasing velocities during isokinetic strength measurement may result from both a decrease in the muscle's ability to produce tension when its length changes during the contraction (Gasser and Hill, 1924; Fenn and Marsh, 1935; Hill, 1970; Close, 1972) and a disadvantageous change from the optimal joint angle at which peak torque is achieved (Thorstensson et al., 1976; Perrine and Edgerton, 1978; Coyle et al., 1979; Fugl-Meyer et al., 1979; Gregor et al., 1979; Scudder, 1980). Relative to the latter factor, a progressive increase in the amount of lever arm movement from the starting position until the time of peak torque registration was found as the velocity of contraction was increased. This finding was also reported for knee extension strength testing on the Cybex by Thorstensson et al. (1976) and Scudder (1980). A time lag between the start of a muscular contraction and the attainment of the pre-set isokinetic velocity, that increases with faster velocities, may partly explain these findings. It may be that at high isokinetic velocities subjects are not able to get the involved limbs moving quickly enough to reach the pre-set velocity before the optimal joint position for strength has been passed. The peak torque values were registered at extended joint positions at the highest velocities used in this study. The influence of this factor on unilateral and bilateral contractions is compared below.

It appeared that each of the two above factors contributed to the decrease in peak torque production that occurred as the velocity of contraction was increased (Perrine and Edgerton, 1978). However, it was observed that the lever arm position at the time of peak torque registration was similar for unilateral and bilateral contractions through the range of test velocities. Hence, the influence of joint angle on peak torque values was comparable between these two conditions.

Thus, in the unilateral condition subjects were not achieving higher peak torques because they were producing their peak torques sooner in the movement, at a more optimum joint angle. Rather, they were producing more tension at an equivalent joint angle of the unilateral and bilateral muscular contractions. This has some bearing on the previously mentioned work regarding the apparent advantage of a high proportion of FT muscle fibres for strength production during dynamic isokinetic muscular contraction in which these two factors have been discussed (Thorstensson et al., 1976, 1977; Coyle et al., 1979; Gregor et al., 1979).

It appeared from the data of Gregor et al. (1979) that the advantage of a relatively higher composition of FT muscle fibre in their subjects became evident at a slow velocity of contraction, when the change in torque from isometric to dynamic contraction was considered. In the present investigation, the finding of a lesser decline from isometric values in the unilateral peak torque than in the bilateral condition at slow velocities of contraction is thus consistent with the hypothesis that there was a greater activation of FT motor units in the unilateral muscular contraction. The differences between unilateral and bilateral muscular contraction became wider as the velocity of contraction was increased to higher levels. This was also consistent with the work of Thorstensson et al. (1976, 1977); Coyle et al. (1979) and Gregor et al. (1979) who found that the positive correlation between FT muscle fibre composition and dynamic torque production became stronger as the velocity of contraction was increased.

It was also observed in the present investigation that the maximal average velocity that subjects could achieve through 10-90% of the range of motion of the leg press movement was greater for unilateral muscular contraction than bilateral. This data is consistent with the studies by Thorstensson et al. (1976) and Larsson et al. (1979). Maximal knee extension velocity correlated positively with %FT fibres in the former study and %FT glycolytic fibres in the latter. The maximal average velocity of unilateral leg presses was found to be significantly greater than bilateral values in the present investigation.

(c) Average torque and impulse. The average torque and impulse of summed unilateral contractions were found to be significantly greater than the bilateral values at all test velocities. Nilsson et al. (1977) have reported a significant positive correlation between the % FT fibre composition of the vastus lateralis muscle and the average torque and impulse of knee extension contractions done at a velocity of 180 °/s.

It was also found that the decline in the B/U ratio for average torque and impulse values was similar to that for peak torque through the range of test velocities. At the highest test velocity of 424 °/s, the summed unilateral work done was almost twice the bilateral value. Thus, the other mechanical measures of torque production also provided evidence of relatively greater tension production in unilateral muscular contraction as the velocity of contraction was increased.

(d) Summary. It appeared from the comparison of the strength-velocity relation of unilateral and bilateral muscular contraction, that there was a greater activation of fast-twitch motor units in the unilateral condition, thereby resulting in the lesser decline in unilateral strength as the velocity of contraction was increased. The structural characteristics which give the fast-twitch motor unit an advantage over the slow-twitch motor unit in dynamic tension production have not yet been clearly identified. Rather, it is an empirical type of knowledge that the FT motor unit has a greater capacity for tension development under dynamic conditions. Evidently, the FT muscle fibre is better able to make and break cross-bridge linkages between the actin and myosin filaments as they slide rapidly by one another as the muscle shortens in dynamic concentric contraction, thereby producing greater tension. The mechanisms responsible for this difference between the 2 fibre types remain to be identified.

It is also known that the fast-twitch motor unit has a lesser resistance to fatigue than the slow-twitch motor unit (see Burke and Edgerton, 1975 for a review and also Garnett et al., 1978). The consistency of the study comparing the fatigability of unilateral and bilateral muscular contraction with the conclusion derived from the strength-velocity comparisons, that there was greater activation of fast-twitch motor units in the unilateral condition, is discussed below.

2. Fatigability of Unilateral and Bilateral Muscular Contraction

(a) Fatigability Results. There was a significant difference between the mean peak torques of summed unilateral and bilateral muscle contractions at the start of the fatigue test; the mean B/U strength ratio was 0.797. This lesser bilateral strength was also observed at the same contraction velocity in the strength-velocity results. The B/U ratios of peak torque were in good agreement between these two testing situations. The fact of this lesser bilateral strength suggested that there was lesser activation of motor units in the bilateral muscular contraction at the start of the fatigue test, as discussed above.

The decline in the peak torque of the bilateral contractions, relative to the start, over the 100 consecutive contractions of the fatigue test was significantly less than the summed unilateral decline. Thus, the peak torque of the bilateral contractions became closer to the summed unilateral value over the course of the fatigue test and the mean B/U ratio of peak torques had increased to 0.931 at the end. Thorstensson and Karlsson (1976), Nilsson et al. (1978), Tesch et al.

(1978) and Komi and Tesch (1979) have all reported significant positive correlations between the amount of decline of peak torque during a knee extension fatigue test and the proportion of fast-twitch muscle fibre in the vastus lateralis muscle. The lesser peak torque at the start of the fatigue tests, but higher resistance to fatigue of the bilateral muscular contractions, is suggestive that there was a lesser activation of FT motor units than in unilateral contractions.

It was noted in this study that differences in the fatigability of unilateral and bilateral muscular contraction were evident after only 10 contractions of the fatigue test. The conclusion that there was a lesser activation of FT motor units in bilateral efforts is consistent with the study of Komi and Tesch (1979). They reported that fatigue was delayed until the 7-10th contraction in their group of subjects identified as having a relatively low FT muscle fibre composition in the vastus lateralis muscle; also, fatigue was already present in the group with a relatively higher FT muscle fibre composition. This rapid onset of fatigue suggested that there was an activation of FT motor units that were capable of a limited number of contractions before the cessation of their firing (Warmolts and Engel, 1972; Burke and Edgerton, 1975; Garnett et al., 1978).

The exact site of the fatigue process in a muscular contraction, whether central or peripheral, has been the subject of considerable investigation (Edwards, 1978). McComas (1977: 71) contended that the site depends on the duration of the exercise. That is, in a short-term situation of a few muscular contractions, fatigue might be expected to occur due to an inability of the central nervous system to maintain the excitement level of the alpha motoneurons, a phenomenon which has been demonstrated in the quadriceps muscles (Bigland-Ritchie et al., 1978). While this would explain the differences in fatigability of the unilateral and bilateral contractions in the early phase of the fatigue test, some other process of fatigue must have been present to differentiate between the two types of contraction later in the test. The site of this fatigue process might be expected to be peripherally located at this duration of the test: either at the neuromuscular junction or in the muscle fibre itself (McComas, 1977: 71).

It has been suggested by Nilsson et al. (1977), that fatigue in their isokinetic knee extension fatigue tests occurred because the excitation-contraction coupling process was impaired. Their observations were based on EMG recordings of fatiguing muscle which showed that the excitation of the muscle fibre was maintained while the strength of contraction declined. Other authors have attributed this impairment to a build-up of lactate that occurred mainly in the FT muscle fibres (Sahlin, 1978; Tesch et al., 1978b, 1978c; Tesch, 1980). The ST muscle fibres would be less likely to accumulate lactate due to a greater capacity for aerobic metabolism (Burke and Edgerton, 1975) in combination with a denser capillary network surrounding the ST fibre (Andersen, 1975) to take away lactate (Tesch et al., 1978a).

It is relevant to note that the blood flow to either leg is decreased during bilateral muscular contraction as compared to unilateral muscular contraction (Gleser, 1973), but despite this, the bilateral fatigability was less. This suggested that in the unilateral muscular contractions, this increased blood flow was not beneficial to those motor units which were undergoing greater activation, relative to the bilateral condition, for resistance to fatigue. If these units were slow-twitch, rather than fast-twitch, greater fatigability would be expected in the bilateral condition, but as noted above, the fatigability results of this investigation were opposite to this.

After 75 contractions of the fatigue test, the peak torque of unilateral and bilateral muscular contractions did not decrease further. This was perhaps evidence of the phenomenon reported by Jones et al. (1979), that in the adductor pollicus muscle, force generation may be optimized in sustained maximal voluntary contraction by a progressive reduction in the firing frequency of motoneurons. It may also be that at this stage of the fatigue test the motor units that were still active were receiving adequate blood flow to prevent further fatigue. Thus, both mechanisms may have contributed to this plateau in fatigue level.

(b) Summary. The fatigability of dynamic bilateral muscular contraction was found to be less than in the unilateral condition. This finding, in combination with the observation that the peak torque of bilateral muscular contraction was less than in the unilateral condition at the start of the fatigue test, suggested that there was a lesser activation of motor units in the bilateral contractions. Based on the previous research discussed above, it was concluded that the motor units undergoing greater activation in unilateral efforts were of the fast-twitch type. The fatigability results of this study are in good agreement with the previously discussed strength-velocity results, in which it was also concluded that fast-twitch motor units were activated to a greater extent in unilateral muscular contraction. This conclusion suggests that the increased maximal voluntary strength of unilateral contractions as compared to bilateral was due to a greater activation of FT motor units in the unilateral type of contraction. One question that arises is: were the available slow-twitch motor units fully activated in the unilateral muscular contraction before these additional fast-twitch motor units were activated? This question is discussed below in relation to previous research on the subject of the order of activation of motor units during increasingly forceful muscular contraction.

C. Conclusions on Patterns of Motor Unit Activation in the Leg Press

Evidence has been presented above to suggest that during dynamic muscular contractions in the leg press movement, there was greater fast-twitch motor unit activation in the unilateral contractions than in the bilateral. It was not known whether this type of pattern of activation also explains the lesser bilateral force development during isometric contractions. Secher et al. (1978), for example, concluded (based on the results of experiments using the drugs d-tubocurarine (dtc) and decamethonium (C_{10}) to selectively block the ST or FT motor units respectively) that the ST motor units were being restricted during the bilateral muscle contractions, thereby causing the demonstrated bilateral loss of force.

This pattern of motor unit activation for isometric contractions has not been found in many human electrophysiological studies however. Several investigators have reported that the smaller motor units (with low discharge frequencies), that are thought to be type 1 slow-twitch units (Warmolts and Engel, 1972), were activated whenever the larger fast-twitch motor units were activated (Buchthal and Schmalbruck, 1970; Person and Kudina, 1972; Warmolts and Engel, 1972; Milner-Brown et al., 1973a; Gydikov and Kosarov, 1974; Desmedt and Godaux, 1977a, 1979; Maton, 1980). It appeared however that there was inconsistency in the results of Secher et al. (1978), between the two drug manipulations. It seems more likely that in the maximal voluntary contractions tested in this study, all ST motor units were being activated in the involved muscles. It is suggested that the ten per cent difference in strength between summed unilateral and bilateral contractions was mostly due to differences in the amount of activation of the large, highly fatigable FT units.

It appears that investigations that used the technique of monitoring glycogen depletion patterns in different types of muscle fibre, in order to study activation patterns, have limited application to this problem, as the metabolic activities of fast and slow-twitch fibres would seem to be different (Burke and Edgerton, 1975; Gollnick et al., 1980). That is, if the glycogen depletion of the 2 fibre types is compared after a short period of voluntary exercise, and for example, there is a greater depletion of the glycogen stores in the FT muscle fibres, it would not be known whether this was due to a greater usage of those fibres, or due to the FT muscle fibre's enhanced capacity to utilize glycogen for energy. Furthermore, the ST muscle fibre could be sparing its glycogen supply by metabolizing lipid sources of energy (Gollnick et al., 1974; Essen et al., 1975; Gollnick et al., 1980).

Evidence was found to suggest that there was a greater activation of FT motor units during dynamic unilateral leg presses. The order of recruitment of motor units during dynamic contractions, whether orderly or not, has been the subject of considerable controversy in the literature (Burke and Edgerton, 1975; McComas, 1977: 66). It would seem functional in one sense for the central nervous system to be able to selectively recruit the fast-twitch muscle fibre with its faster and stronger twitch properties (Burke and Tsairis, 1973; Burke and Edgerton, 1975; Edgerton, 1976) for rapid force production. However, the more fatigue-resistant slow-twitch motor unit, with a contraction time to peak tension of approximately twice that of the FT unit (Buchthal and Schmalbruck, 1970; Sica and McComas, 1971; Burke and Edgerton, 1975; Garnett et al., 1978) is still functional at relatively high velocities of movement (Smith et al., 1980), although less so than the FT unit. The organization of the motor system may thus be biased to initially activate motor units in voluntary muscular contraction that have the highest oxidative metabolic capacity (Burke and Edgerton, 1975).

The order of recruitment of motor units, from slow-twitch to fast-twitch, may not be firmly fixed however, and some exceptional subjects may be able to selectively recruit fast-twitch motor units before slow-twitch units (Grimby and Hannerz, 1977). Desmedt and Godaux criticized this study though, on the basis that statistical proof of their findings was not present. In a recent publication these latter authors have advanced evidence that there was an orderly recruitment of motor units in both isometric and dynamic contractions in a finger abduction movement (Desmedt and Godaux, 1979).

Desmedt and Godaux (1979) also advanced an explanation of how erroneous conclusions on the order of recruitment of motor units during dynamic contractions could have been made in previous investigations, where the temporal order of motor unit action potentials recorded at the muscle was taken to represent the recruitment order of motor units. The faster conduction velocity of the larger motor axon of the larger motor unit, from the spinal cord to the muscle, may result in its motor unit spike occurring in the muscle before the smaller motor unit's spike occurs, although the smaller motor unit was actually recruited first.

Based on the above published research, it was concluded that FT motor units were not "preferentially recruited" (Desmedt and Godaux, 1977b) over ST motor units in either the unilateral or bilateral muscular contractions done under isometric and dynamic conditions. It was postulated that the same ST motor units were recruited in unilateral and bilateral contractions. Further, in the unilateral condition there was an additional activation of motor units, and based on the comparison of the strength-velocity relation and fatigability of unilateral and bilateral muscular contraction, it was concluded that these additionally activated units exhibited characteristics that identified them as being of the fast-twitch type. Why this additional recruitment of motor units occurred in unilateral muscular contraction remains an unanswered question (see below).

D. Mechanism for Additional Motor Unit Activation in Unilateral Muscular Contraction

The activation of a motor unit depends upon the attainment of a critical amount of depolarization of the cell body of its motoneuron residing in the ventral horn of the spinal cord. This depolarization is the result of a greater facilitatory influence on the cell body than the inhibitory influence, both of which could be present (Guyton, 1976:68). Both of these influences (greater facilitation and lesser inhibition) could be responsible for the activation of additional motor units in the unilateral condition. That is, the addition of a second limb in a bilateral contraction may decrease the level of excitability of the spinal motoneuron pool of the involved muscles of either leg due to a peripheral inhibition effect caused by reflexes crossing the spinal cord (Perl, 1958, 1959; Lagasse, 1974; Morris, 1974; Guyton, 1976: 135). The decrease may also result from a lessening of the descending central facilitating input, because the concentration or "mental energy" (Brodal, 1973) needed to activate motor units has been divided over two limbs.

Although it was not possible to separate these two influences in this investigation, one observation seems pertinent (this would appear to be a possible future direction of research regarding the unilateral/bilateral strength phenomenon). It may be that when the above problem of the relative contribution of peripheral and central effects on the decreased bilateral motor unit activation is considered with regard to high velocity contractions, the peripheral effect may be minimal. The short time of the contraction and the preprogrammed ballistic nature of the contraction may have precluded proprioceptive input to the spinal motoneuron (Lagasse, 1974; Morris, 1974; Desmedt and Godaux, 1979; Maton, 1980).

In either condition of isometric and slow dynamic contractions, or high velocity contractions, a decrease in the level of excitation of the spinal motoneuron pool would be postulated to particularly affect motoneurons of the FT motor units. These motoneurons, because of their larger size and hence lower input resistance, require a greater excitatory input than ST motoneurons to create a sufficient depolarization of the cell membrane to the threshold level for discharging (Henneman et al., 1965). This mechanism may have been responsible for the apparent lesser activation of FT motor units in bilateral muscle contraction.

V. SUMMARY

The purpose of the present study was to investigate the reported observation that there was a lesser maximal voluntary isometric strength in bilateral, as compared to summed unilateral, leg extension muscular contraction. The present investigation expanded previous research on this phenomenon by using electromyographical techniques to study the apparent lesser motor unit activation in the bilateral condition. Leg extension was studied under isometric and concentric contraction conditions. Furthermore, by using a comparison of the strength-velocity relation and fatigability of unilateral and bilateral contractions, evidence was obtained regarding the question of which type of motor unit was being activated to a lesser extent in bilateral contractions. The results are summarized below.

The EMG evidence collected indicated that there was a lesser activation of motor units in bilateral contractions made in isometric, and low and high velocity concentric conditions. The ratio of recorded bilateral to unilateral electrical activity did not decrease as the velocity of contraction was increased, although the bilateral to unilateral strength ratio did. This indicated that the amount of motor unit activation deficit in bilateral efforts did not increase with velocity increases, but rather that those motor units activated in bilateral contractions became less able to produce tension at high velocity relative to the unilateral condition.

Evidence that there was a lesser activation of fast-twitch motor units in bilateral contractions, was obtained by comparing the strength-velocity relation of the two types of contraction when a range of selected velocities from 0°/s to 424°/s was used. The B/U strength ratio declined from 0.91 under isometric conditions to 0.78 at a low 15°/s velocity and further through the range of velocities to 0.51 at the highest test velocity of 424°/s. Other mechanical measures of the strength of bilateral and unilateral contractions, average torque and impulse, also showed this greater decline in bilateral strength as the velocity of contraction was increased. Complementary to these results, the fatigability of bilateral contractions was found to be less than unilateral over the course of 100 fatiguing concentric contractions.

The results of both the strength-velocity and fatigability comparisons supported the conclusion that there was a lesser activation of fast-twitch motor units in bilateral as compared to unilateral muscle contraction.

REFERENCES

Andersen, P. (1975) Capillary density in skeletal muscle of man. Acta Physiol. Scand. 95: 203-205.

Asmussen, E., K. Heeboll-Nielsen and S. Molbech (1959) Methods for evaluation of muscular strength. Comm. Dan. Nat. Ass. for Infant. Paral. No. 5a.

Asmussen, E. and K. Heeboll-Nielsen (1961) Isometric muscle strength of adult men and women. Comm. Dan. Nat. Ass. for Infant. Paral. No. 11.

Awad, E. A. and F. J. Kottke (1964) Effectiveness of myotatic reflex facilitation in augmenting rate of increase of muscular strength due to brief maximal exercise. Arch. Phys. Med. Rehabil. 45: 23-29.

Barrett, J. N. and W. E. Crill (1971) Specific membrane sensitivity of dye-injected cat motoneurons. Brain Res. 28: 556-561.

Barrett, J. N. and W. E. Crill (1974) Specific membrane properties of cat motoneurons. J. Physiol. 239: 301-324.

Basmajian, J. V. (1977) Motor learning and control: a working hypothesis. Arch. Phys. Med. Rehabil. 58: 38-41.

Basmajian, J. V., T. P. Harden and E. M. Regenos (1972) Integrated actions of the four heads of quadriceps femoris: An electromygraphic study. Anat. Rec. 172: 15-19.

Bigland, B. and O. J. C. Lippold (1954) The relation between force, velocity and integrated electrical activity in human muscles. J. Physiol. 123: 214-224.

Bigland-Ritchie, B., D. A. Jones, G. P. Hosking and R. H. T. Edwards (1978) Central and peripheral fatigue in sustained maximum voluntary contractions of human quadriceps muscle. Clin. Sci. Mol. Med. 54: 609-614.

Brodal, A. (1973) Self-observations and neuro-anatomical considerations after a stroke. Brain 96: 675-694.

Brooke, M. H. and K. K. Kaiser (1974) The use and abuse of muscle histochemistry. Ann. N. Y. Acad. Sci. 228: 121-144.

Buchthal, F. and H. Schmalbruch (1980) Motor unit of mammalian muscle. Physiol. Rev. 60: 90-142.

Buchthal, F., and H. Schmalbruch (1970) Contraction times and fibre types in intact human muscle. Acta Physiol. Scand. 79: 435-452.

Burke, R. E. and P. Tsairis (1973) Anatomy and innervation ratios in motor units of cat gastrocnemius. J. Physiol. 234: 749-765.

Burke, R. E. and V. R. Edgerton (1975) Motor unit properties and selective involvement in movement. In: Exercise and Sport Sciences Reviews. Ed. J. F. Keogh and J. H. Wilmore. New York: Academic Press, pp. 31-81.

Close, R. I. (1972) Dynamic properties of mammalian skeletal muscles. Physiol. Rev. 52: 129-196.

Clough, J. F. M., C. G. Phillips, and J. D. Sheridan (1971) The short-latency projection from the baboon's motor cortex to fusimotor neurons of the forearm and hand. J. Physiol. 216: 257-279.

Coleman, A. E. (1969) Effect of unilateral isometric and isotonic contractions on the strength of the contralateral limb. Res. Quart. 40: 490-495.

Coyle, E. F., D. L. Costill and G. R. Lesmes (1979) Leg extension power and muscle fibre composition. Med. Sci. Sports 11: 12-15.

Desmedt, J. E. and E. Godaux (1977a) Ballistic contractions in man: characteristic recruitment patterns of single motor units of the tibialis anterior muscle. J. Physiol. 264: 673-693.

Desmedt, J. E. and E. Godaux (1977b) Fast motor units are not preferentially activated in rapid voluntary contractions in man. Nature 267: 717-719.

Desmedt, J. E. and E. Godaux (1979) Voluntary motor commands in human ballistic movements. Ann. Neurol. 5: 415-421.

Easton, T. A. (1972) On the normal use of reflexes. Am. Sci. 60: 591-599.

Edgerton, V. R. (1976) Neuromuscular adaptation to power and endurance work. Can J. Appl. Sport. Sci. 1: 49-58.

Edgerton, V. R., J. L. Smith and D. R. Simpson (1975) Muscle fibre type populations of human leg muscles. Histochem. J. 7: 259-266.

Edwards, R. H. T. (1978) Physiological analysis of skeletal muscle weakness and fatigue. Clin. Sci. Mol. Med. 54: 463-470.

Eloranta, V. and P. V. Komi (1980) Function of the quadriceps femoris muscle under maximal concentric and eccentric contractions. Electromyogr. Clin. Neurophysiol. 20: 159-174.

Essen, B., E. Jansson, J. Henriksson, A. W. Taylor and B. Saltin (1975) Metabolic characteristics of fibre types in human skeletal muscle. Acta Physiol. Scand. 95: 153-165.

Fenn, W. O. and B. S. Marsh (1935) Muscular force at different speeds of shortening. J. Physiol. 85: 277-297.

Fugl-Meyer, A. R., M. Sjostrom and L. Wahlby (1979) Human plantar flexion strength and structure. Acta Physiol. Scand. 107: 47-56.

Gans, B. M. and A. Noordergraff (1975) Voluntary skeletal muscles: a unifying theory on the relationship of their electrical and mechanical activities. Arch. Phys. Med. Rehabil. 56: 194-199.

Garnett, R. A. F., M. J. O'Donovan, J. A. Stephens and A. Taylor (1978) Motor unit organization of human medial gastrocnemius. J. Physiol. 287: 33-43.

Gasser, H. S. and A. V. Hill (1924) The dynamics of muscular contraction. Pro. Roy. Soc. Lon. B. 96: 398-437.

Gleser, M. A. (1973) Effects of hypoxia and physical training on hemodynamic adjustments to one-legged exercise. J. Appl. Physiol. 34: 655-659.

Gollnick, P. D., K. Piehl, and B. Saltin (1974) Selective glycogen depletion pattern in human muscle fibres after exercise of varying intensity and at varying pedalling rates. J. Physiol. 241: 45-58.

Gollnick, P. D., L. Hermanesen and B. Saltin (1980). The muscle biopsy: still a research tool. Phys. Sports Med. 8: 50-55.

Granit, R. (1970) The Basis of Motor Control. New York: Academic Press.

Gregor, R. J., V. R. Edgerton, J. J. Perrine, D. S. Campion and C. DeBus (1979) Torque-velocity relationships and muscle fibre composition in elite female athletes. J. Appl. Physiol. 47: 388-392.

Grimby, L. and J. Hannerz (1977) Firing rate and recruitment order of toe extensor motor units in different modes of voluntary contraction. J. Physiol. 264: 865-879.

Grimby, L., J. Hannerz and B. Hedman (1979) Contraction time and voluntary discharge properties of individual short toe extensor motor units in man. J. Physiol. 289: 191-201.

Guyton, A. C. (1976) Structure and Function of the Nervous System. Second Edition. Philadelphia: W. B. Saunders Co.

Gydikov, A. and D. Kosarov (1974) Some features of different motor units in human biceps brachii. Pflugers Arch. 347: 75-88.

Gydikov, A., G. Dimitrov, D. Kosarov and N. Dimitrova (1976) Functional differentiation of motor units in human opponens pollicus muscle. Exp. Neurol. 50: 36-47.

Hayes, K. C. and A. M. Clarke (1978) Facilitation of late reflexes in humans during the preparatory period of voluntary movement. Brain Res. 153: 176-182.

Hellebrandt, F. A., A. M. Parrish and S. J. Houtz (1947) Cross education: the influence of unilateral exercise on the contralateral limb. Arch. Phys. Med. Rehabil. 28: 76-85.

Hellebrandt, F. A. (1951) Cross-education: ipsilateral and contralateral effects of unimanual training. J. Appl. Physiol. 4: 136-144.

Hellebrandt, F. A., S. J. Houtz and R. N. Eubank (1951) Influence of alternating and reciprocal exercise on work capacity. Arch. Phys. Med. Rehabil. 32: 766-776.

Hellebrandt, F. A. and J. C. Waterland (1962) Indirect learning: influence of unimanual exercise on related muscle groups of same and opposite side. Am. J. Phys. Med. 41: 45-55.

Henneman, E. (1974) Organization of the spinal cord. In: Medical Physiology. Thirteenth Edition. Volume 1. Ed. V. B. Mountcastle. St. Louis: C. V. Mosby Co., pp. 636-650.

Henneman, E. and C. B. Olson (1965) Relations between structure and function in the design of skeletal muscles. J. Neurophysiol. 28: 581-598.

Henneman, E., G. G. Somjen and D. O. Carpenter (1965) Functional significance of cell size in spinal motoneurons. J. Neurophysiol. 28: 599-620.

Hill, A. V. (1970) First and Last Experiments in Muscle Mechanics. London: Cambridge University Press.

Houston, M. E. (1978) The use of histochemistry in muscle adaptation: a critical assessment. Can. J. Appl. Sport. Sci. 3: 109-118.

Hunt, C. C. and E. R. Perl (1960) Spinal reflex mechanism concerned with skeletal muscle. Physiol. Rev. 40: 538-579.

Ikai, M. and A. H. Steinhaus (1961) Some factors modifying the expression of human strength. J. Appl. Physiol. 16: 157-163.

Imms, F., A. J. Hackett, S. R. Prestidge and R. H. Fox (1977) Voluntary muscle strength of patients undergoing rehabilitation following fractures of the lower limb. Reumatol. and Rehabil. 16: 162-171.

Johnson, M. A., J. Polgar, D. Weightman and D. Appleton (1973) Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. J. Neurol. Sci. 18: 111-119.

Jones, D. A., B. Bigland-Ritchie and R. H. T. Edwards (1979) Excitation frequency and muscle fatigue: mechanical responses during voluntary and stimulated contractions. Exp. Neurol. 64: 401-413.

Kimura, J. (1977) Electrical activity in voluntarily contracting muscle. Arch. Neurol. 34: 85-88.

Knapik, J. J. and M. U. Ramos (1980) Isokinetic and isometric torque relationships in the human body. Arch. Phys. Med. Rehabil. 61:64-67.

Komi, P. V. and P. Tesch (1979) EMG frequency spectrum, muscle structure, and fatigue during dynamic contractions in man. Eur. J. Appl. Physiol. 42: 41-50.

Lagasse, P. P. (1974) Ipsilateral and contralateral effects of superimposed stretch. Arch. Phys. Med.Rehabil. 55: 305-310.

Larsson, L., G. Grimby and J. Karlsson (1979) Muscle strength and speed of movement in relation to age and muscle morphology. J. Appl. Physiol. 46: 451-456.

Logan, G. A. and A. Lockhart (1962) Contralateral transfer of specificity of strength training. J. Am. Phys. Ther. Assoc. 42: 658-660.

McComas, A. J. (1977) Neuromuscular Function and Disorders. London: Butterworths.

Mathews, D. K., C. T. Shay. F. Godin and R. Hogdon (1956) Cross transfer effects of training on strength and endurance. Res. Quart. 27: 206-212.

Matthews, P. B. C. (1972) Mammalian Muscle Receptors and Their Actions. Baltimore: Williams and Wilkins.

Maton, B. (1980) Fast and slow motor units: their recruitment for tonic and ~~phasic contraction~~ action in normal man. Eur. J. Appl. Physiol. 43: 45-55.

Milner-Brown, H. S., R. B. Stein and R. Yemm (1973a) The orderly recruitment of human motor units during voluntary isometric contractions. J. Physiol. 230: 359-370.

Milner-Brown, H. S., R. B. Stein and R. Yemm (1973b) Changes in firing rate of human motor units during linearly changing voluntary contractions. J. Physiol. 230: 371-390.

Milner-Brown, H. S. and R. B. Stein (1975) The relation between the surface electromyogram and muscular force. J. Physiol. 246: 549-569.

Moffroid, M., R. Whipple, J. Hofkosh, E. Lowman and H. Thistle (1969) A study of isokinetic exercise. Phys. Ther. 49: 735-746.

Moore, J. C. (1975) Excitation overflow: an electromyographic investigation. Arch. Phys. Med. Rehabil. 56: 115-120.

Moritani, T. and H. A. DeVries (1979) Neural factors versus hypertrophy in the time course of muscle strength gain. Am. J. Phys. Med. 58: 115-130.

Morris, A. F. (1974) Myotatic reflex effects on bilateral reciprocal leg strength. Am. Corr. Ther. J. 28: 24-29.

Nilsson, J., P. Tesch and A. Thorstensson (1977) Fatigue and EMG of repeated fast voluntary contractions in man. Acta Physiol. Scand. 101: 194-198.

Patton, R. W., M. M. Hinson, B. R. Arnold, and B. Lessard (1978) Fatigue curves of isokinetic contractions. Arch. Phys. Med. Rehabil. 59: 407-509.

Perl, E. A. (1958) Crossed reflex effects evoked by activity in myelinated afferent fibres of muscle. J. Neurophysiol. 21: 101-112.

Perl, E. A. (1959) Effects of muscle stretch on excitability of contralateral motoneurons. J. Physiol. 145: 193-203.

Perrine, J. J. and V. R. Edgerton (1978) Muscle force-velocity and power-velocity relationships under isokinetic loading. Med. Sci. Sports 10: 159-166.

Person, R. S. and L. P. Kudina (1972) Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. Electroenceph. Clin. Neurophysiol. 32: 471-483.

Peter, J. B., R. J. Barnard, V. R. Edgerton, C. A. Gillespie and K. E. Stempel (1972) Metabolic profiles of three fibre types of skeletal muscle in guinea pigs and rabbits. Biochem. 11: 2627-2633.

Pollack, V. (1980) Surface EMG and muscle force at low force levels. Am. J. Phys. Med. 59: 126-141.

Provins, K. A. (1955) Maximum forces exerted about the elbow and shoulder joints on each side separately and simultaneously. J. Appl. Physiol. 7: 390-392.

Roush, E. S. (1951) Strength and endurance in the waking and hypnotic state. J. Appl. Physiol. 3: 404-410.

Rube, N., N. H. Secher and F. Lodberg (1979) The effect of habituation and training on two and one leg extension strength. Acta Physiol. Scand. 108: 8A.

Sahlin, K. (1978) Intracellular pH and energy metabolism in skeletal muscle of man. With special reference to exercise. Acta Physiol. Scand. Suppl. 455.

Sale, D. G. (1979) The effect of training and immobilization upon neuromuscular function in man. Unpublished Ph.D. thesis, McMaster University.

Sale, D. G. (December, 1979) Personal Communication. Re: An unpublished weight training study by G. Moran at McMaster University.

Saltin, B., J. Henriksson, E. Nygaard and P. Andersen (1977) Fibre types and metabolic potentials of skeletal muscles in sedentary man and endurance runners. Ann. N. Y. Acad. Sci. 301: 3-29.

Scudder, G. N. (1980) Torque curves produced at the knee during isometric and isokinetic exercise. Arch. Phys. Med. Rehabil. 61: 68-72.

Secher, N. H. (1975) Isometric rowing strength of experienced and inexperienced oarsmen. Med. Sci. Sports 7: 280-283.

Secher, N. H., S. Rorsgaard and O. Secher (1976) Contralateral influence on recruitment of type 1 muscle fibres during maximal voluntary extension of the legs. Acta Physiol. Scand. 96: 20A-21A.

Secher, N. H., S. Rorsgaard and O. Secher (1978) Contralateral influence on recruitment of curarized muscle fibres during maximal voluntary extension of the legs. Acta Physiol. Scand. 103: 456-462.

Shaver, L. G. (1970) Effects of training on relative muscular endurance in ipsilateral and contralateral arms. Med. Sci. Sports 2: 165-171.

Shaver, L. G. (1973) Muscular endurance in ipsilateral and contralateral arms: influence of training and inactivity. Arch. Phys. Med. Rehabil. 54: 505-509.

Sherrington, C. S. (1906) The Integrative Action of the Nervous System. New Haven: Yale University Press.

Sica, R. E. P. and A. J. McComas (1971) Fast and slow twitch units in a human muscle. J. Neurol. Neurosurg. Psychiat. 34: 113-120.

Slater-Hammel, A. T. (1950) Bilateral effects of muscle activity. Res. Quart. 21: 203-209.

Smith, L. E. (1970) Facilitatory effects of myotatic strength training upon leg strength and contralateral transfer. Am. J. Phys. Med. 49: 131-141.

Smith, J. L., B. Betts, V. R. Edgerton, and R. F. Zernicke (1980) Rapid ankle extension during paw shakes: selective recruitment of fast ankle extensors. J. Neurophysiol. 43: 612-620.

Stein, R. B. (1974) Peripheral control of movement. Physiol. Rev. 54: 215-243.

Tesch, P. (1980) Muscle fatigue in man with special reference to lactate accumulation during short term intense exercise. Acta Physiol. Scand. Suppl. 480.

Tesch, P., B. Sjodin and J. Karlsson (1978a) Relationship between lactate accumulation, LDH activity, LDH isozyme and fibre type distribution in human skeletal muscle. Acta Physiol. Scand. 103: 40-46.

Tesch, P., L. Larsson, A. Eriksson and J. Karlsson (1978b) Muscle glycogen depletion and lactate concentration during downhill skiing. Med. Sci. Sports 10: 85-90.

Tesch, P., B. Sjodin, A. Thorstensson and J. Karlsson (1978c) Muscle fatigue and its relation to lactate accumulation and LDH activity in man. Acta Physiol. Scand. 103: 413-420.

Thorstensson, A. (1976) Muscle strength, fibre types and enzyme activities in man. Acta Physiol. Scand. Suppl. 443.

Thorstensson, A. and J. Karlsson (1976) Fatigability and fibre composition of human skeletal muscle. Acta Physiol. Scand. 98: 318-322.

Thorstensson, A., G. Grimby and J. Karlsson (1976) Force-velocity relations and fibre composition in human knee extensor muscles. J. Appl. Physiol. 40: 12-16.

Thorstensson, A., L. Larsson, P. Tesch and J. Karlsson (1977) Muscle strength and fibre composition in athletes and sedentary men. Med. Sci. Sports 9: 26-30.

Viitasalo, J. T., and P. V. Komi (1978) Force-time characteristics and fibre composition in human leg extensor muscles. Eur. J. Appl. Physiol. 40: 7-15.

Walters, C. E. (1955) Effect of overload on bilateral transfer of motor skill. Phys. Ther. Rev. 35: 567-569.

Warmolts, J. R. and W. K. Engel (1972) Open-biopsy electromyography. Arch. Neurol. 27: 512-517.

Wolf, S. L. (1979) The morphological and functional basis of therapeutic exercise. In: Therapeutic Exercise, Third Edition. Ed. J. V. Basmajian. Baltimore: Williams and Wilkins, pp. 1-32.

APPENDIX

A. Reproducibility of Measurements

1. Voluntary Strength. The overall method error of 11.4% for the measurement of peak torque of the leg press movement on the modified Cybex on 2 separate days was similar to the method error of 13.7% reported for the measurement of peak torque of a knee extension movement on a conventional Cybex apparatus by Thorstensson *et al.* (1976). Other investigators have reported high accuracy and reliability with isokinetic Cybex testing of maximal voluntary strength in a variety of movements (Moffroid *et al.*, 1969; Patton *et al.*, 1978; Coyle *et al.*, 1979; Larsson *et al.*, 1979; Knapic and Ramos, 1980 and Scudder, 1980). The reproducibility of leg press peak torque values is shown in Table 1 of the appendix.

The overall method error for the B/U ratio of peak torques over 2 separate days was 8.5% (see also Appendix Table 1). This method error for the measurement of this variable has not been previously reported in the literature. The B/U ratio appeared to be a stable phenomenon, reproducible over separate testing occasions, particularly at low contraction velocities.

The method errors of measurement for peak torque, average torque and impulse, which are compared in Table A-1, were all greater at the higher test velocity than the lower test velocity. This was also found by Sale (1979) for the same measures in the movements of ankle plantar flexion, knee extension and elbow extension (knee extension

Table 1. Reproducibility of measurement of voluntary strength made on two separate days.

	Velocity (°/s)	Summed Unilateral M.E. (V, %)	Bilateral M.E.(V,%)	B/U Ratio M.E.(V,%)
Peak Torque	15	8.2	10.3	5.8
	380	13.1	17.9	11.1
Average Torque	15	6.4	8.7	5.1
	380	17.1	20.6	13.3
Impulse	15	7.2	9.2	2.9
	380	21.9	29.7	13.5

Values were calculated with 8 subjects.

average torque was an exception). This phenomenon has not been previously discussed in the literature. One possible explanation for the increased method errors at the high velocity is that the pattern of force development was different at the 2 velocities. The force output during high velocity contractions was dependent on a rapid development of force in the short duration of the contraction, whereas in a slow contraction, more time was used to develop tension. The results of high velocity contractions would thus appear to more dependent on a rapid recruitment of the largest FT motor units at the start of the contraction. However, these motor units are considered to be the most difficult to recruit during a maximal voluntary contraction (Sale, D. G., personal communication), and, they may not have been consistently activated over separate days and even over repeated trials. The method errors for the leg press and bench press peak torque, average torque and impulse measurements made over repeated trials were also found to be larger at the higher contraction velocity.

The variation in duplicate determinations of maximal voluntary strength comes from both methodological and biological sources (Thorstensson et al., 1976). The method error for the measurement of maximal voluntary strength made on repeated trials was found to be less than that for measurements made on separate days. This might be due to a decrease in the variation from both of the above sources. As the biological factor is mainly the result of the amount of motivation and cooperation give by subjects during the test sessions (Sale, 1979) and perhaps a learning factor as well, a randomized order of limbs tested and velocities of contraction was used to avoid any order of testing effects. Further, subjects were given warm-up trials to familiarize them with contraction velocity before the measurement of maximal effort was made. This may have resulted in the low method errors found for measurements made over repeated trials (See Appendix Table 2).

Method errors of similar size were found for the measurement of peak torque, average torque and impulse. Sale (1979) reported the same finding. The largest method errors of measurements made in the study were found for average torque and impulse measurements made during high velocity contractions. A possible effect of increasing velocity on the method error of measurement is discussed above. Further, the variables of average torque and impulse depend on the torque exerted over the entire duration of the contraction and the method error of measurements of average torque and impulse tended to be slightly larger than those of peak torque measurement (Table 3).

The method errors for the summed unilateral measurements of maximal voluntary strength were of a similar size to those made for bilateral contractions. The overall method error for the variable of the B/U ratio, of peak torque, average torque, and impulse measures made on two separate days was 8.6%, which was consistent with other values of reproducibility. The reproducibility of the B/U ratio of average torque and impulse values has not been previously reported in the literature. It was found in this study that the B/U ratio of all 3 measurements, peak torque, average torque and impulse was a consistent phenomenon, comparable in reproducibility to previously reported measures of knee extension strength.

2. <u>Maximal Average Velocity</u>. The measure of maximal average velocity through 10 to 90% of the range of motion proved to be a

Table 2. Reproducibility of peak torque measurements and B/U ratios made on repeated trials.

Velocity (°/s)	Summed Unilateral M.E.(V,%)	Bilateral M.E.(V,%)	B/U Ratio M.E.(V,%)
0	3.1	4.2	5.0
15	1.9	5.6	5.6
30	2.9	1.3	4.0
52.5	1.9	3.9	4.0
105	1.5	4.0	3.3
216	1.5	(234[1]) 2.3	-
332	3.1	3.6	4.8
380	3.7	5.0	5.6
424	5.2	7.5	7.7

Values were calculated with 9 subjects

[1]Bilateral Velocity

Table 3. Reproducibility of average torque and impulse measurements and B/U ratios made on repeated trials.

	Velocity (°/s)	Summed Unilateral M.E.(V,%)	Bilateral M.E.(V,%)	B/U Ratio M.E.(V,%)
Average Torque	15	2.5	2.0	4.1
	380	4.4	8.8	11.3
Impulse	15	1.6	2.2	2.2
	380	5.0	9.8	15.3

Values were calculated with 9 subjects.

highly reproducible variable as reflected in the low method error. Thorstensson (1976) reported a day to day method error of 5.2% for the measurement of maximal knee extension velocity, a figure very close to that found in this study for the leg press movement.

3. Fatigue Tests. The method error of 6.8% for the variable of endurance ratio, after 50 contractions in the bilateral leg fatigue test, was larger than the 3.2% method error reported by Thorstensson (1976) for single leg knee extension. The method error for the leg press fatigue tests in this study was the same after 50 or 100 contractions.

Table 4. Reproducibility of measurement of maximal average velocity through 10-90% of the range of motion, made on repeated trials and on two separate days

	Left M.E.(V,%)	Right M.E.(V,%)	Bilateral M.E.(V,%)
Repeated Trials	1.3	2.3	2.2
Two Separate Days	5.5	4.5	4.9

Values were calculated with 9 subjects, repeated trials; 8 subjects, two separate days.

ANALYSIS OF VARIANCE TABLE - MEASURE: INTEGRATED EMG ACTIVITY

Source	SS	df	MS	F	p
Type of Contraction	1.64	1	1.64	11.75	$<.006$
Cases x Type C.	1.53	11	0.14		
Velocity	57.69	2	28.84	128.10	$<.001$
Cases x Vel.	4.95	22	0.23		
Type C. x Vel.	0.15	2	0.08	0.83	$<.448$
Cases x Type C. x Vel.	2.02	22	0.09		

ANALYSIS OF VARIANCE TABLE - MEASURE: PEAK TORQUE

Source	SS	df	MS	F	p
Type of Contraction	474.98	1	474.98	146.07	$< .001$
Subj. x Type C.	26.01	8	3.25		
Velocity	15191.16	7	2170.17	327.35	$< .001$
Subj. x Vel.	371.26	56[a]	6.63		
Type C. x Vel.	21.01	7	3.00	4.01	$< .001$
Subj. x Type C. x Vel.	41.90	56[a]	0.75		

[a]Includes four estimated values.

ANALYSIS OF VARIANCE TABLE - MEASURE: AVERAGE TORQUE

Source	SS	df	MS	F	p
Type of Contraction	280.00	1	280.00	250.06	$<.001$
Subj. x Type C.	8.96	8	1.12		
Velocity	7382.65	6	1230.44	495.23	$<.001$
Subj. x Vel.	119.26	48[a]	2.49		
Type C. x Vel.	6.71	6	1.12	2.87	$<.018$
Subj. x Type C. x Vel.	18.72	48[a]	0.39		

[a]Includes four estimated values.

ANALYSIS OF VARIANCE TABLE - MEASURE: IMPULSE

Source	SS	df	MS	F	p
Type of Contraction	6.64	1	6.64	151.12	<.001
Subj. x Type C.	0.35	8	0.04		
Velocity	667.30	6	111.22	1447.89	<.001
Subj. x Vel.	3.69	48[a]	0.08		
Type C. x Vel.	0.69	6	0.12	8.08	<.001
Subj. x Type C. x Vel.	0.69	48[a]	0.01		

[a]Includes four estimated values.

ANALYSIS OF VARIANCE - MEASURE: FATIGUE

Source	SS	df	MS	F	p
Type of Contraction	92.63	1	92.63	101.33	$<.001$
Subj. x Type C.	7.31	8	0.91		
Number of Contractions	482.27	5	96.45	71.99	$<.001$
Subj. x No. C.	53.59	40	1.33		
Type C. x No. C.	20.34	5	4.07	17.66	$<.001$
Subj. x Type C. x No. C.	9.22	40	0.23		