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RELEVANCE OF *IN VIVO* FORCE MEASUREMENTS TO HUMAN BIOMECHANICS

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Abstract—The function and mechanical behaviour of human skeletal muscle are in many ways unknown during natural locomotion. To gain more insight into these questions a method was developed to record directly *in vivo* forces from the human Achilles tendon (AT). The paper focuses on the details of the various techniques including the design, surgical implantation and calibration of the transducers. The implantation is performed under local anaesthesia and the measurements can last up to three hours, after which the transducer is removed. Exemplar results are presented from the measurements during walking, running and jumping. The loading of AT reached in some cases values as high as 9 KN, corresponding to 12.5 times the body weight or, when expressed per cross-sectional area of the tendon, the value was 11 100 N cm^{-2}. During the early contact phase of running the rate of AT force development increased linearly with the increase of running speed. Indirect measurements of the length changes of the muscle–tendon complex was used to plot the force–length and force–velocity relationships in the various activity situations. The observed results demonstrated that in normal locomotion involving the stretch–shortening cycle (SSC) muscle actions, the mechanical response of the triceps surae muscle is very different from the classical curves obtained in isolated muscle preparations. In agreement with the animal experiments using a similar *in vivo* technique, the natural locomotion with primarily SSC actions may produce muscle outputs which can be very different from the various conditions of the isolated preparations, where activation levels are held constant and storage and utilization of strain energy is limited. It is suggested that despite some limitations (due to e.g. difficulties in obtaining volunteers for AT force measurements, possible inaccuracies in transducer calibration and in muscle length estimates) the *in vivo* force measurement technique has an important role in studying the mechanical behaviour of muscle and its control under normal movement conditions.

INTRODUCTION

Information on the forces produced by individual skeletal muscles or muscle groups during normal locomotion is important to the understanding of muscle mechanics, muscle physiology, musculoskeletal mechanics, neurophysiology and motor control. A great number of reports have appeared in the literature, describing as accurately as possible these forces and their relationships to total joint movement. The methods applied produce different estimates and the applications can therefore also be different. The methods used to determine these forces have been both direct and indirect. Indirect estimation can refer to such methods as the mathematical solution of the actual muscle force in the indeterminate musculoskeletal system. This requires grouping muscles in order to reduce the number of unknowns for the appropriate equations of motion (e.g. Paul, 1965). Prediction of individual muscle torques by electromyography has been performed for the triceps surae (Hof and van den Berg, 1977) as well as for the elbow flexor muscles. The primary problem for use of electromyography is its sensitivity to varying conditions of muscle action types, velocity of contraction, fatigue, training and detraining. A similar problem may exist when one wants to apply various methods of optimization during dynamic movements (e.g. Crowninshield and Brand, 1981; Herzog, 1987). The validation of the method applied is thus the major question to remain unsolved in all of the methods of indirect measurement.

Can forces of individual muscles during locomotion be measured directly? Despite natural problems of inaccuracy the general answer to this question is positive. Since Salmons (1969) introduced a design of the buckle transducer for recording tendon forces in animals a number of experiments have been performed to measure individual muscle forces in cat (e.g. Walmsley *et al.*, 1978; Whiting *et al.*, 1984; Gregor *et al.*, 1988) and monkey (Peres *et al.*, 1983) locomotion. These buckle type transducers are surgically implanted on selected tendons and after an appropriate healing and recovery period, *in vivo* recordings can be performed under a range of movement conditions. This approach has been applied recently to human subjects, in which the transducer has been implanted around the Achilles tendon (Komi *et al.*, 1987). The present report deals with these human experiments with an attempt to describe the applications as well as to analyze critically the advantages and disadvantages.

METHODS

Basic technical development

The application of an *in vivo* measurement technique for humans required several stages of development and trials with animals (for details see Komi *et al.*, 1987). These stages included such technical questions as transducer designs, details of surgical operation and duration of implantation. In these

preliminary experiments with rabbits, no inflammatory tissue reaction was observed even when the duration of implantation was more than one week. For this reason and also because transducer response remained similar throughout the follow-up periods, preparations were soon made to develop the transducer for experiments on human beings. The first problem was to find a suitable tendon for such experiments. It appeared that the human Achilles tendon was suitable for implantation and recording for the following reasons: (1) the space between the tendon and the bone (Karger triangle) is relatively large and the transducer would not touch the bone surface even during extreme dorsiflexion of the foot; (2) the surgical procedure itself is fairly simple and comparable to cleaning of adhesions around the tendon from patients suffering from tendonitis. However, the selection of the Achilles tendon has some limitations, because it is a common tendon for triceps surae complex including both soleus and gastrocnemius muscles, of which the gastrocnemius is a two-joint muscle.

The first experiment utilized the *E*-form transducer which was implanted under local anaesthesia around the Achilles tendon of an adult male. The transducer was kept *in situ* for seven days and the eighth day was used for testing. During the one-week post-operation period the pain did not disappear completely and for this reason the experiments were limited to simple plantar flexion movements against a force plate and to slow walking. No running or jumping exercises could be performed. A short abstract of the paper has been published (Komi *et al.*, 1984) and the details of the transducer design and dimensions and a summary of the results have been presented elsewhere (Komi *et al.*, 1987). This experiment was a necessary step for further transducer development. The calibration of the transducer was not solved by the time of the experiment and therefore it could not be performed. In addition there were other important aspects which needed attention. First of all, the transducer was too big in size and the silicon material covering the transducer frame was not smooth enough. These two factors were responsible for the pain not disappearing during the seven-day period during which the transducer was kept in place.

Research methodology with a buckle-type transducer

The many problems which the first prototype transducer brought to light delayed progress towards new measurements by approximately one year. This period was used to finalize the transducer design. Its size was made much smaller and it was coated not with silicon but instead with a thin layer of gold, which made the transducer surface corrosive-resistant and also very smooth. A collection of prototypes was prepared until the final decision was made to select the buckle transducer, originally introduced by Salmons (1969), and later modified for measurements from the tendon of the common digital extensor muscle of the horse

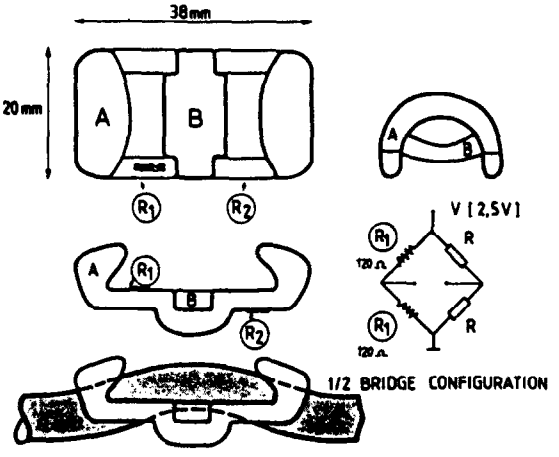

Fig. 1. Schematic presentation of the 'buckle'-type transducer designed for experiments in which human subjects could perform even maximal activities, e.g., in running and jumping. (A) Main buckle frame; (B) cross-bar. R_1 and R_2 = resistors of the 1/2 Wheatstone bridge configuration. The lower part demonstrates schematically (and with slight exaggeration) the bending of the Achilles tendon when the transducer is *in situ*.

(Barnes and Pinder, 1974) and for experiments on cat gastrocnemius (e.g. Sherif *et al.*, 1983). The transducer consists of a main 'buckle' frame, two strain gauges, and a centre bar placed across the frame (Fig. 1). The frame and the centre bar are moulded from stainless steel. Three different sizes of frame are available and each frame has three different kinds of cross-bar. The differences in frame size and in cross-bar bending ensures that a suitable transducer is available for almost any size of adult human Achilles tendon. In order to assist in the selection of the best possible transducer size, the ankle of the subject is first X-rayed (lateral view) before surgery. The final selection is performed during the operation, when the tendon is visible and can be easily palpated and the thickness measured again. In order to avoid possible sideways movement of the buckle the width of the tendon must match as closely as possible the interior width of the buckle frame. So far, no special quantification criteria have been used to select the cross-bar, which fixes the tendon onto the buckle frame. However, a slight bend in the tendon is necessary for transducer function. If the bending is excessive the tendon structures may suffer damage. The transducer shown in Fig. 1 shows a frame of middle size (38 mm in length, 20 mm in width, and 13.5 mm in height). Figure 1 also shows the sites on which the standard foil strain gauges (MM 120 Ω) were bonded. The second half Wheatstone bridge configuration was located outside the skin surface. The wires were made of Teflon R-coated copper strand (CZ 1105 Cooner Wire Co.).

Implantation

All the procedures including surgical implantation were reviewed and accepted by the ethical committee of the hospital responsible.

Fig. 2. The X-ray side view showing the 'buckle' transducer around the Achilles tendon.

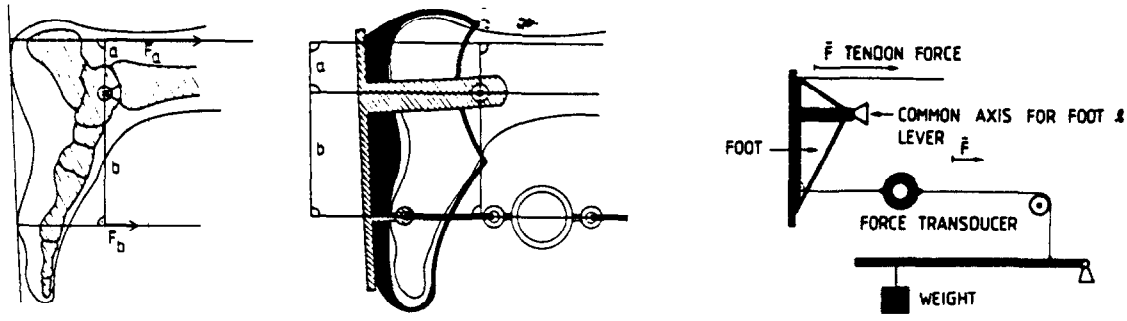

Fig. 3. Geometrical arrangements to demonstrate the force couple on the foot and its application in a special shoe system which was fastened to a calibration table (not shown in the figure). The entire system was fastened to the end of the table, and calibration weights, including the respective force transducers, were placed under the table. The subject was lying prone on the table.

The transducer is implanted under local anaesthesia in normal male subjects who sign a written agreement to volunteer as subjects. During the surgery, which lasts 15–20 min, the subject is in a prone position on the operating table. 15–20 ml 1 % lidocaine with adrenaline (4 g ml^{-1}) is injected around the calcanear tendon. In order to provide normal proprioception during movements, lidocaine is not injected into the tendon or the muscle tissue. Evidence has been presented that when local anaesthesia is injected directly into the muscle the myoelectric response of the muscle could be affected (e.g. Inoue and Frank, 1962; Sabbahi *et al.*, 1979). An incision of approximately 50 mm in length is made on the lateral side just anterior to the tendon to avoid damage to the small saphenous vein and the sural nerve. The size of the buckle is matched with that of the tendon. The correct sized cross-bar is then placed under the tendon into the slots of the frame. This causes a small bend in the tendon as demonstrated schematically in the lower part of Fig. 1. The cable containing the wires from the strain gauges are threaded under the skin and brought outside approximately 10 cm above the transducer. After the cut is sutured and carefully covered with sterile tapes, the cable of the transducer is connected to an amplifying unit for immediate checkup. Figure 2 demonstrates a lateral X-ray view of the transducer *in situ*.

Calibration of the transducer

Although the details of the calibration procedure have been presented earlier (Komi *et al.*, 1987), they are also explained in detail here. Calibration is perhaps one of the most critical parts of an experiment of this nature.

In animal experiments, the calibration is performed during the terminal experiment with the gauges *in situ* on their tendons. The appropriate tendon is then cut distally to the transducer and tied to another force-measuring unit. By applying electrical stimulation to a freely dissected nerve, the transducer can be calibrated either under static (Walmsley *et al.*, 1978) or dynamic (e.g. Sherif *et al.*, 1983) external loading conditions.

In experiments with human subjects it must be noted that calibration is not as simple as in animal experiments. For the present series of experiments a more indirect calibration was used. After the transducer was securely in place and the wound sutured and covered with sterile tapes, the subject was placed on a special calibration table. His operated foot was then placed in a special shoe, which is fastened onto a freely rotating frame, the axis of which coincides with that of the ankle joint. A pulley system with known weights was used to dorsiflex the foot. The direction of the pull was parallel to the Achilles tendon. Taking into consideration the geometrical arrangements of the transducer, axis of rotation, and the pulley system, the exact values of Achilles tendon forces could be calculated. The dynamic response of the Achilles tendon could be calibrated by adding the spring system between the strain gauge and the weight of the dorsiflexing cable.

The geometric arrangements of Fig. 3 give an ideal picture of the situation. However, it must be emphasized that this arrangement needs to be prepared carefully and individually for each subject. Even a small variation in the angle of pull of the tendon as well as in the common axis for foot and lever arm will introduce considerable errors in the absolute force levels. Figure 4 presents representative records of the transducer response to external loading. As can be seen the transducer followed even the small changes in the external load well. When several loads are used the calibration procedure lasts 10–15 min. Figure 5 represents a typical calibration curve for a static loading condition. As can be seen from the figure, the curve is slightly concave and the maximum calibration voltage has reached the level recorded for the concentric action during maximal squatting jumps.

EXEMPLAR RESULTS

Measurements with the implanted tendon transducer can last as long as the local anaesthesia is effective. In practice this usually means 2–3 h, after which the size of the tendon is measured either with

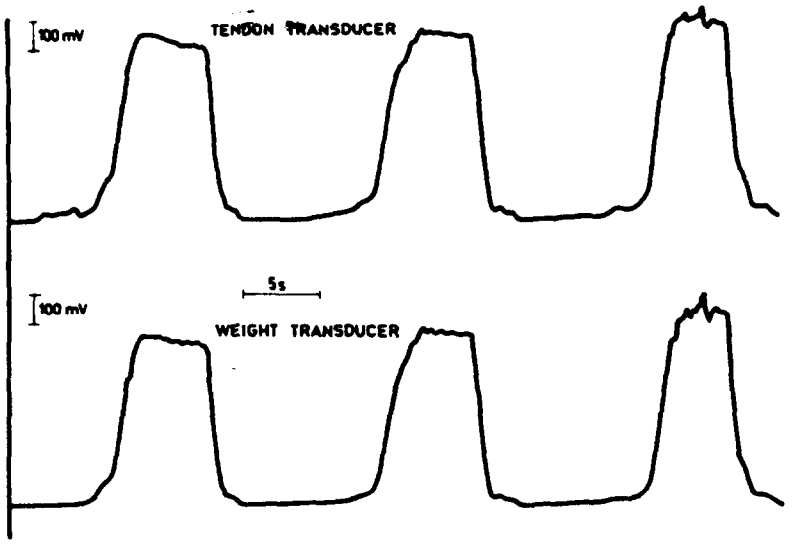

Fig. 4. Examples of the responses of the tendon transducer and force transducer (calibration weight) when weights were added successively during the calibration procedure.

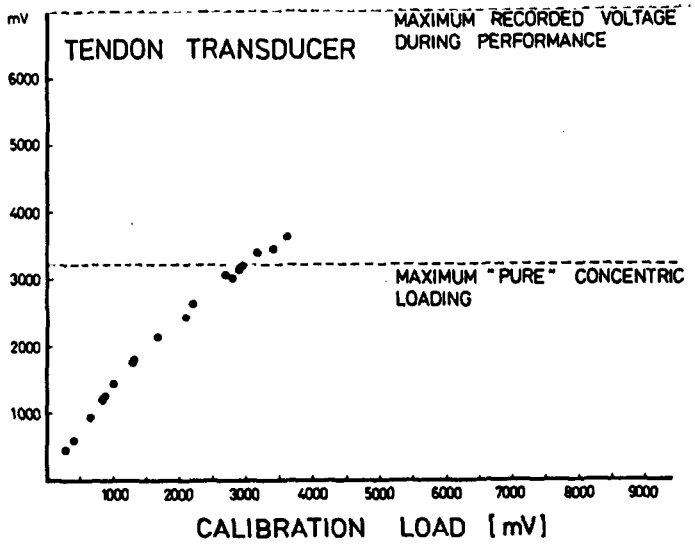

Fig. 5. A typical curve for static calibration of the Achilles tendon transducer.

computer tomography or ultrasound as well as manually during the final removal operation. The measurements have included activities from normal slow walking to running, jumping, sprinting and bicycling. These measurements have also included simultaneous recordings of ground reaction forces on a 10–12 m long force platform as well as electromyographic (EMG) activities from the selected muscles of the ipsilateral leg.

Walking and running

Figure 6 gives an example of walking on the long force platform at various constant speeds ranging from 1.2 to 1.8 m s^{-1}. Each individual curve represents an averaged curve of a minimum of four ipsilateral contacts. In this example the peak-to-peak amplitude of Achilles tendon force (ATF) is very much the same across all speeds, whereas the rate of ATF development is greater at high walking speeds. Another important feature in the ATF response is the sudden release of force upon the heel contact on the force plate. The heel contact occurs at the point of increase in the vertical (F_z) and forward–backward (F_y) curves of the force plate reaction forces. Figure 7 represents two examples from running: one with the ball contact (left) and the other with the heel contact (right) of the same subject. It is evident from these curves that heel

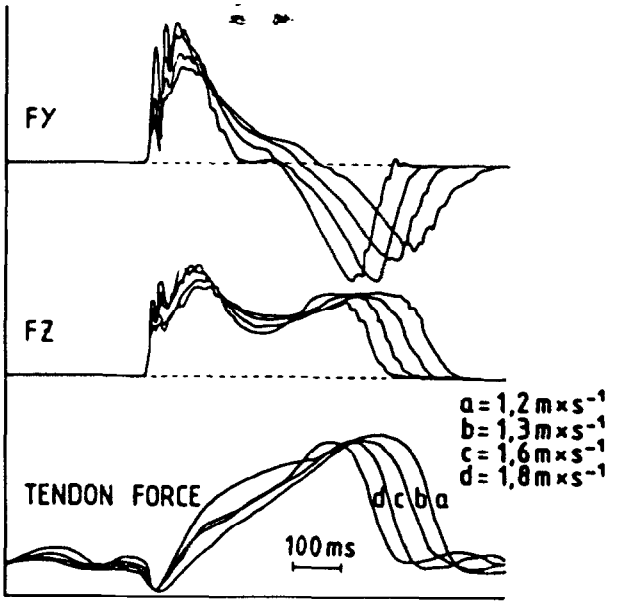

Fig. 6. Achilles tendon force curves during walking at different speeds. The beginning of the upward reflection of the ground reaction force curves (*Fz* and *Fy*) shows the heel contact. Force and time units are not shown.

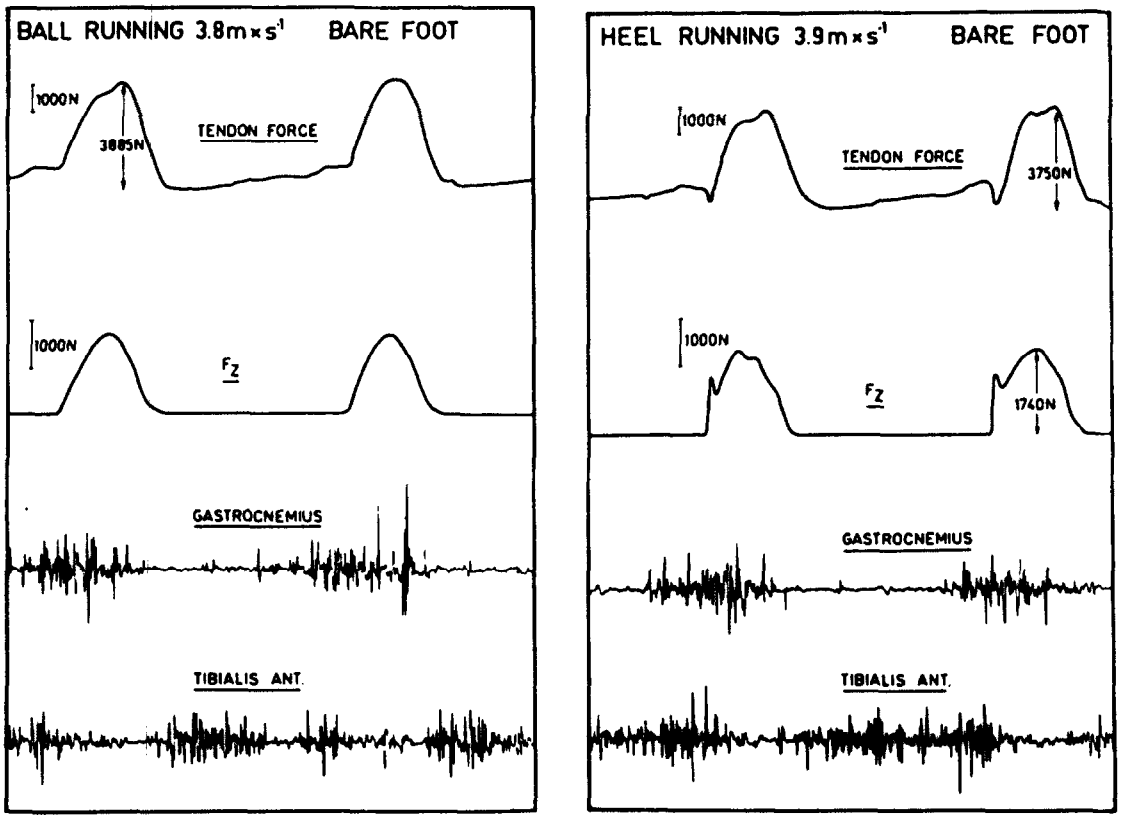

Fig. 7. Example of bare foot running with ball (left) and heel contact (right). Note the sudden release of tendon force upon heel contact on the force plate.

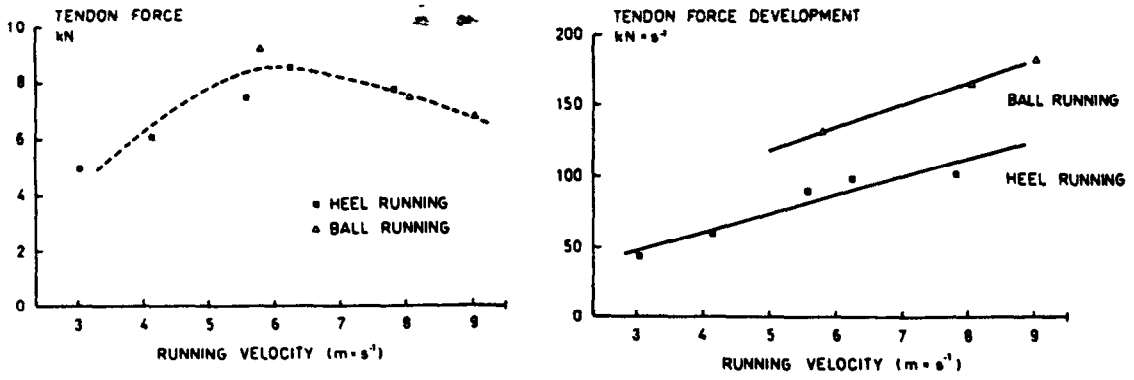

Fig. 8. Peak tendon forces (left) and peak rates of tendon force development (right) for one subject running at different velocities.

contact running is characterized by a very quick release of ATF upon heel contact. This coincides with the release of EMG activation of the tibialis anterior muscle resulting in a reduction in stretch of the Achilles tendon. The velocity of plantarflexion is then probably momentarily greater than the shortening velocity of the active soleus and gastrocnemius muscles.

Figure 8 presents, again for one subject only, peak (left) and maximum rates (right) of ATF when the subject ran at different speeds using both techniques of foot contact. The maximum ATF seems to have already attained its highest value at a speed of 6 m s^{-1}, in which case the value was 9 kN corresponding to 12.5 BW. When the cross-sectional area of the tendon was 0.81 cm^2, the peak force for this subject was 11 100 N cm^{-2}, a value which is well above the range of the single load ultimate tensile strength (Butler *et al.*, 1984). The qualitative presentation of Fig. 8 shows that the maximum rates of ATF development, measured during the sharp rising phase after the contact, increased linearly with the increase in running velocity during contact.

Force–length and force–velocity curves during contact phase in running and jumping

In vivo recording of ATFs can also be applied to measurements of various mechanical parameters for the triceps surae muscle. In order to do this one must first get an estimation of the segmental length changes of the muscle–tendon complex. In our experiments the method of Grieve *et al.* (1978) was used for this purpose. This method requires filming the performance perpendicular from the side view. The angular displacements of both knee and ankle joint are then computed and the values are then used in the formula provided by Grieve *et al.* (1978) to predict the segmental length changes for both gastrocnemius and soleus muscles. Figure 9 provides examples of the segmental length changes of the gastrocnemius in two long jump performances, one performed submaximally and the other with almost maximal effort. In both cases the gastrocnemius muscle–tendon complex shortens upon the heel strike at the same time as ATF is suddenly released. Thereafter the muscle is put under stretch and while it is active it functions eccentrically. The eccentric action ends approximately at the same time as the peak ATF. The shortening phase (concentric action) then follows at a very fast rate, slightly faster than the decrease in ATF. Changes in force and length can then be computed to observe how the stiffness coefficient ($\Delta F/\Delta l$) changes for the contact phase in long jump take off (Kyröläinen *et al.*, 1989).

Figure 10 presents an analysis for the force/length and force/velocity curves during the contact phase in running. The force–length curve demonstrates a very sharp increase in force during the stretching phase, which is characterized by a small change in length. The right-hand side shows the force/velocity comparison demonstrating high potentiation during the stretching phase (concentric action). If these curves are compared with the force–velocity curves obtained with isolated muscle preparations (e.g. Hill, 1938) or with human forearm flexors (e.g. Komi, 1973) the dissimilarities are evident. It must be noted that these force–length and force–velocity curves of Fig. 10 are instantaneous plots during the stretch–shortening cycle (SSC) and may therefore represent more truly the behaviour of the muscles during natural movements. If the subject is running on two occasions at similar speeds the analysis gives remarkably similar results. Running at near maximum speed (9.02 m s^{-1}) seemed to result in lower peak ATF but the length change in the eccentric phase was much smaller (Fig. 10). In many of our observations in running, the length change in gastrocnemius and soleus usually occurs in parallel with the stretching phase ending simultaneously. This is in contrast to cycling, where the similarity is not so clear. The utilized muscle length estimation has, however, demonstrated that in cycling these muscles also function in a stretch–shortening cycle (Gregor *et al.*, 1988), although the stretching phases are not as apparent as in running or jumping.

As introduced by Grieve *et al.* (1978) the plots shown in Fig. 10 can be complemented with EMG

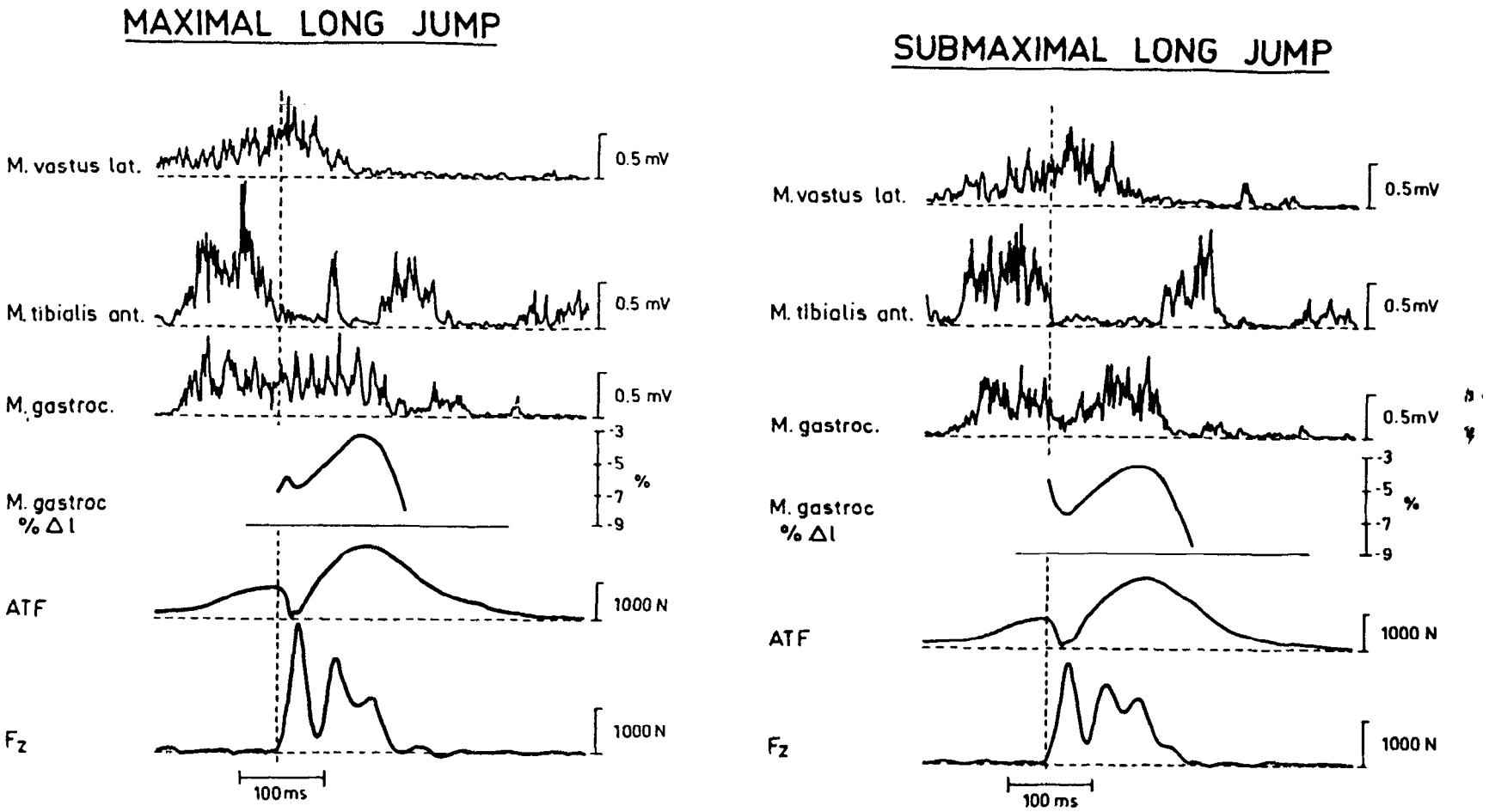

Fig. 9. Rectified EMGs, length of the gastrocnemius (GA) muscle and Achilles tendon force (ATF) during take-off contact in the good (left) and medium (right) jump. The vertical broken line signifies the moment of the first heel contact of the take-off leg. In the record of the change in the gastrocnemius length, the upward direction indicates increase (stretch) and the downward direction decrease (shortening).

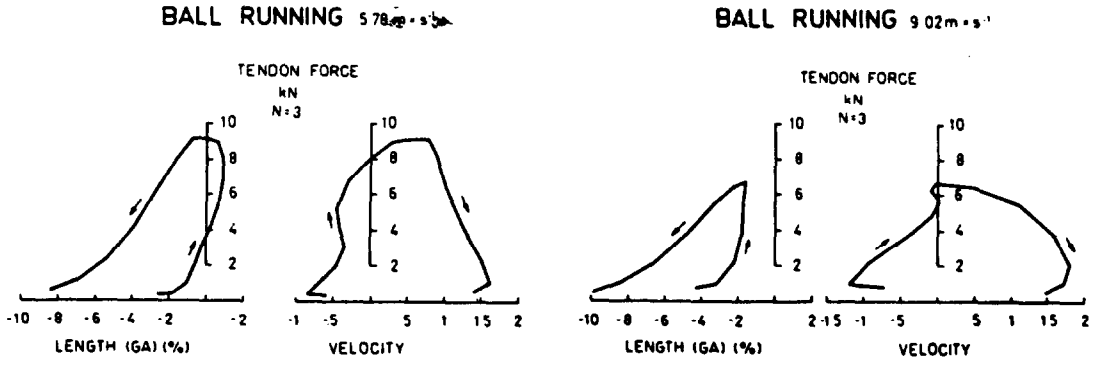

Fig. 10. Force–length and force–velocity curves of the gastrocnemius (GA) muscle for the ground contact phase when a subject ran with ball contact at two different velocities: 5.78 m s^{-1} and 9.02 m s^{-1}. The curves begin at the ball strike and the arrows indicate the direction (from stretch to shortening).

analysis, in which case the EMG integral can be plotted against muscle length or against velocity of action (stretching and shortening).

DISCUSSION

It seems evident that *in vivo* recording of Achilles tendon forces can be used to analyze several important parameters in muscle mechanics, such as peak forces, rates of force development, and force–length and force–velocity responses. It may, however, be possible to extend application to such an analysis as reflex response during natural type movements. In the stretch–shortening cycle (SSC) actions the stretch reflex activation can be interpreted as the servo mechanism to control stiffness behaviour of leg extensor muscles (Dietz *et al.*, 1981; Gollhofer *et al.*, 1984). The major problem in a natural exercise condition is the correct recording of the force response during the entire process of the reflex action. ATF-recording in the manner presented in this report could prove useful in this regard. This would certainly be another interesting application which would complement the others, aimed primarily at revisiting the important question of muscle mechanics.

In vivo registration requires a surgical procedure, which in principle is simple, but which may cause ethical problems. Our experience has, however, proved that the risks in the entire procedure including the operation are minimal provided that special care is also taken to secure sterile conditions during measurements. The size of the buckle transducer must also be selected carefully. The form of the cross-bar determines how much the tendon will be bent. A slight bending is necessary, but excessive bending could cause too much unnecessary stretch in the wrong directions, and it may even damage the tendon at higher stretch loads. The quantitative criteria for correct sizing of the transducer including the cross-bar are lacking.

The selection of the Achilles tendon was based primarily on two factors: (1) application of the transducer around the tendon is simple and during movement the transducer will not touch the bony structures; (2) running, walking and jumping are the most natural activities and those which are characterized as SSC actions for the triceps surae muscle. It must be noted, however, that ATF-measurements cannot separate the two muscles—soleus and gastrocnemius, of which the gastrocnemius muscle is a two-joint muscle. Fortunately, in most situations of running and jumping, the stretching and shortening phases occur in phase in these two muscles. Bicycling, however, is different from these activities.

In human biomechanics—in contrast to studies with cats—the *in vivo* tendon technique is not yet so well developed that the long-term adaptation studies can be performed while the transducer is *in situ* for several months. More experience is needed before efforts are made to involve larger groups of subjects for this type of experiment. It is, however, quite possible to re-implant the transducer around the same Achilles tendon and repeat the measurements at certain intervals. In any case the calibration of the transducer is important for all experiments which require knowledge of exact forces. In studies which are planned for investigating time sequence and the interaction of EMG with force components in specific movements, some compromise could be accepted for calibration accuracy. Improvement of the calibration procedure is also important if one wants to use the *in vivo* technique for verification of other methods of tendon force measurement, such as mathematical modelling.

One additional feature of *in vivo* tendon force measurements needs attention: in many studies of muscle mechanics one may want to separate the muscular and tendon components with regard to range and velocities of stretch and shortening. The muscle lengths presented in the material of this report are merely to indicate the potential use of the gastrocnemius and soleus muscles. It must be recognized that more work is needed to identify more exactly

when the muscle fibres are shortening or whether the tendon is shortening or whether both are acting in different directions and yield a net effect at the end points of either lengthening or shortening. For this specific purpose the current use of estimating the length changes of this total muscle/tendon system from film analysis needs to be replaced with other methods which can continuously follow the two components separately. In animal experiments Griffiths (1987) has introduced an ultrasound transit-time technique to record the length changes of the muscle fibres. Hoffer *et al.* (1989) have then applied this method in studying cat walking and have demonstrated that in the medial gastrocnemius muscle the superficial fibres and the tendon do not shorten or stretch in phase. The data showed further that in cat walking the changes in the parent muscle lengths do not reflect the changes in muscle fibre length. The authors emphasize that more accurate estimation of the length changes of the muscle fibre (or muscle spindle) should include muscle architecture, location of the muscle fibre and the external load. It would, therefore, be interesting to see how valid these conclusions are when the piezoelectric ultrasound technique measures deeper muscle fibres. In addition, it is probably of greater importance to utilize activity situations which cause higher muscle stiffness than slow walking. A similar method is certainly worth developing for human experiments.

As indicated in the Introduction the *in vivo* measurement technique for humans has been developed following the reports on animal experiments. In fact the technique of the present human experiments is a direct application of the buckle transducer technique in cats (Sherif *et al.*, 1983). The procedure in animal experiments is, however, different from that in humans in the following aspects: (1) the transducer(s) is(are) left in place around the tendon(s) for several weeks or months and the measurements can therefore be repeated frequently with the same animal; (2) especially in cats, several muscles have been implanted simultaneously and the forces of the soleus and gastrocnemius muscles can be measured separately (e.g. Fowler *et al.*, 1989). Many of the animal experiments have included similar parameters to those described in this report for human experiments such as muscle length, force and EMG (e.g. Goslow *et al.*, 1973; Hodgson, 1983; Sherif *et al.*, 1983; Walmsley *et al.*, 1978; Whiting *et al.*, 1984). In addition, Landjerit *et al.* (1988) have applied buckle transducers to record muscular forces and torques *in vivo* during isometric flexion of the elbow in small monkeys. The most relevant for the comparison with the present human experiments is the report of Gregor *et al.* (1988), who measured mechanical outputs of the cat soleus during treadmill locomotion. In their study the results indicated that the force generated at a given shortening velocity during late stance phase was greater, especially at higher speeds of locomotion, than the output generated at the same shortening velocity, *in situ*. Although the exemplary data presented in this report should not allow excessively broad generalizations, the data in Fig. 9 can be used to suggest that the findings of Gregor *et al.* (1988) and those of the present human experiments are in many ways similar with regard to the force–velocity (F–V) relationships. Although our human experiment did not include the classical F–V measurements, similar to that of the *in situ* measurement of Gregor *et al.* (1988), the form of the curves in Fig. 9 clearly indicates performance potentiation in the concentric action. The difference of the F–V curve from that of the classical curve in isolated muscle preparations (e.g. Hill, 1938) or in human experiments (e.g. Wilkie, 1950; Komi, 1973) may naturally be due to differences in muscle activation levels between the two types of activities, but it can only partly explain the deviations. While the *in situ* preparations may primarily measure the shortening properties of the contractile elements in the muscle, natural locomotion, primarily utilizing SSC action, involves controlled release of high forces, caused primarily by the eccentric action. This high force favours storage of elastic strain energy in the muscle–tendon complex. A portion of their stored energy can be recovered during the subsequent shortening phase. The events and possible mechanisms of the elastic potentiation have been discussed in detail earlier (e.g. Alexander and Bennet-Clark, 1977; Cavagna, 1977; Rack and Westbury, 1974; Komi, 1984). Both animal and human experiments seem to agree that natural locomotion with primarily SSC muscle action may produce muscle outputs which can be very different from various conditions of isolated preparations, where activation levels are held constant and storage of strain energy is limited.

CONCLUDING REMARKS

Continuous and immediately available records of muscle forces are no doubt important in many applications of biomechanics research. *In vivo* tendon force recording is an attempt to make this type of approach possible. By utilizing human subjects it is possible to make well-planned experimental situations and repeat the measured performances several times. The recording transducer and the cables and telemetering units do not prevent the performances from being natural and thus the entire physiological range of movement velocities can be covered. The methodology developed is naturally still subject to criticism. However, the accuracy and applications are likely to be better than those of any more indirect approaches to evaluating individual muscle/tendon forces during locomotion.

REFERENCES

Alexander, R. McN. and Bennet-Clarke, H. C. (1977) Storage of elastic strain energy in muscle and other tissues. *Nature* **265**, 114–117.

Barnes, G. R. G. and Pinder, D. N. (1974) *In vivo* tendon tension and bone strain measurement and correlation. *J. Biomechanics* **7**, 35–42.

Butler, D. L., Grood, E. S., Noyes, F. R., Zernicke, R. F. and Brackett, K. (1984) Effects of structure and strain measurement technique on the material properties of young human tendons and fascia. *J. Biomechanics* **17**, 579–596.

Cavagna, G. A. (1977) Storage and utilization of elastic energy in skeletal muscle. In *Exercise and Sport Science Reviews* (Edited by Hutton, R. W.), Vol. 5, pp. 89–129. Journal Publishing Affiliates, Santa Barbara.

Crowninshield, R. D. and Brand, R. A. (1981) A physiologically based criterion of muscle force prediction in locomotion. *J. Biomechanics* **14**, 793–802.

Dietz, V., Voth, J. and Schmidtbleicher, D. (1988) Interaction between preactivity and stretch reflex in human triceps brachii during landing from forward falls. *J. Physiol.* **311**, 113–125.

Fowler, E. G., Gregor, R. J., Hodgson, J. A., Roy, R. R. and Broker, J. P. (1989) The contribution of individual muscles to the ankle moment produced in the cat hindlimb. *J. Biomechanics* **21**, 1011.

Gollhofer, A., Schmidtbleicher, D. and Dietz, V. (1988) Regulation of muscle stiffness in human locomotion. *Int. J. Sports Med.* **5**, 156–159.

Goslow, G. E., Reinking, R. M. and Stuart, D. G. (1973) The cat step cycle: hindlimb joint angles and muscle lengths during unrestrained locomotion. *J. Morphol.* **141**, 1–42.

Gregor, R. J., Roy, R. R., Whiting, W. C., Hodgson, J. A. and Edgerton, V. R. (1988) Force–velocity potentiation in cat soleus muscle during treadmill locomotion. *J. Biomechanics* **21**, 721–732.

Grieve, D. W., Pheasant, S. and Cavanagh, P. R. (1978) Prediction of gastrocnemius length from knee and ankle joint posture. In *Biomechanics VI-A* (Edited by Asmussen, E. and Jörgensen, K.), pp. 405–412. University Park Press, Baltimore.

Griffiths, R. I. (1987) Ultrasound transit time gives direct measurement of muscle fiber length *in vivo*. *J. Neurosci. Meth.* **21**, 159–165.

Herzog, W. (1987) Individual muscle force estimations using a non linear optimal design. *J. Neurosci. Meth.* **21**, 167–179.

Hill, A. V. (1938) The heat and shortening of the dynamic constant of muscle. *Proc. R. Soc. Lond.*, Series B **126**, 136–195.

Hodgson, J. A. (1983) The relationship between soleus and gastrocnemius muscle activity in conscious cats: a model for motor unit recruitment? *J. Physiol.* **337**, 553–562.

Hof, A. L. and Berg, J. W. van den (1977) Linearity between the weighted sum of the EMGs of the human triceps surae and the total torque. *J. Biomechanics* **10**, 529–539.

Hoffer, J. A., Caputi, A. A., Pose, I. E. and Griffiths, R. I. (1989) Roles of muscle activity and load on the relationships between muscle spindle length and whole muscle length in the freely walking cat. *Progr. Brain Res.* **80**, 75–85.

Inoue, F. and Frank, G. B. (1962) Action of procaine on frog skeletal muscles. *J. Pharmacol. Exp. Ther.* **136**, 190–196.

Komi, P. V. (1973) Measurement of the force–velocity relationship in human muscle under concentric and eccentric contractions. In *Medicine and Sport*, Vol. 8, Biomechanics III, pp. 224–229. Karger, Basel.

Komi, P. V. (1984) Physiology and biomechanical correlates of muscle function: effects of muscle structure and stretch-shortening cycle on force and speed. In *Exercise and Sport Sciences Reviews* (Edited by Terjung, R. H.), Vol. 12, pp. 81–123. D. C. Heath, Lexington, MA.

Komi, P. V., Salonen, M. and Järvinen, M. (1984) *In vivo* measurements of achilles tendon forces in man. ACSM Annual Meeting Abstracts. *Med. Sci. Sports Exercise* **16**, 165–166.

Komi, P. V., Salonen, M., Järvinen, M. and Kokko, O. (1987) *In vivo* registration of achilles tendon forces in man. I. Methodological development. *Int. J. Sports Med.* **8**, 3–8.

Kyröläinen, H., Avela, J. and Komi, P. V. (1989) Regulation of muscle force and stiffness during long jump take-off. *Proc. XII Int. Congr. Biomechanics* (Edited by Gregor, R. J., Zernicke, R. F. and Whiting, W. C.). UCLA, California.

Landjerit, B., Maton, B. and Peres, G. (1988) *In vivo* muscular force analysis during the isometric flexion on a monkey's elbow. *J. Biomechanics* **21**, 577–584.

Paul, J. P. (1965) Bioengineering studies of the forces transmitted by joints (II). *Biomechanics and Related Bioengineering Topics* (Edited by Kenedi, R. M.). Pergamon Press, London.

Peres, G., Maton, B., Lanjerit, B. and Philippe, C. (1983) Electromyographic and mechanical aspects of the coordination between elbow flexor muscles in monkeys. In *Biomechanics VIII-A* (Edited by Matsui, H. and Kobayashi, K.), pp. 455–463.

Rack, P. M. H. and Westbury, D. R. (1974) The short-range stiffness of active mammalian muscle and its effects on mechanical properties. *J. Physiol.* **240**, 331–350.

Sabbahi, M. A., De Luca, C. J. and Powers, W. R. (1979) Effect of ischemia, cooling and local anesthesia on the median frequency of the myoelectric signals. *Proc. 4th Congr. Int. Soc. Electrophysiol. Kinesiol.*, Boston, U.S.A., pp. 94–95.

Salmons, S. (1969) The 8th International Conference on Medical and Biological Engineering—meeting report. *Bio-Med. Engng* **4**, 467–474.

Sherif, M. H., Gregor, R. J., Liu, L. M., Roy, R. R. and Hager, C. L. (1983) Correlation of myoelectric activity and muscle force during selected cat treadmill locomotion. *J. Biomechanics* **16**, 691–701.

Walmsley, B., Hodgson, J. A. and Burke, R. E. (1978) Forces produced by the medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *J. Neurophysiol.* **5**, 535–577.

Whiting, W. C., Gregor, R. J., Roy, R. R. and Edgerton, V. R. (1984) A technique for estimating mechanical work of individual muscles in the cat during treadmill locomotion. *J. Biomechanics* **17**, 685–694.

Wilkie, R. R. (1950) The relation between force and velocity in human muscle. *J. Physiol.* **110**, 249–280.