Journal of Physiology (1991), **437**, *pp.* 287–304
With 6 *figures*
Printed in Great Britain

DYNAMIC CONTROL OF MUSCLE STIFFNESS AND H REFLEX MODULATION DURING HOPPING AND JUMPING IN MAN

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(*Received 14 August 1990*)

SUMMARY

1. The objective of the study was to evaluate the functional effects of reflexes on muscle mechanics during natural voluntary movements. The excitability of the H (Hoffmann) reflex was used as a measure of the excitability of the central component of the stretch reflex.

2. We recorded EMG, ground reaction forces and the H reflex in the soleus muscle in humans while landing from a downward jump, during drop jumping and during hopping. The movements were also recorded by high-speed cinematography.

3. The EMG pattern was adapted to the motor task. When landing the EMG in the soleus muscle and in the anterior tibial muscle showed preinnervation and alternating activity after touch down. When hopping there was little preinnervation in the soleus muscle, and the activity was initiated about 45 ms after touch down by a peak and continued unbroken until lift off. In the drop jumps the EMG pattern depended on the jumping style used by the subject.

4. The H reflex in the soleus muscle was strongly modulated in a manner appropriate to the requirements of the motor task. During landing from a downward jump the H reflex was low at touch down whereas while hopping it was high at touch down. During drop jumping it was variable and influenced by the jumping technique.

5. Muscle stiffness in the ankle joint was negative after touch down when landing, but always positive when hopping.

6. It is suggested that during landing the alternating EMG pattern after touch down was programmed and little influenced by reflexes. During hopping reflexes could contribute to the initial peak and the EMG during lift off.

7. The programmed EMG activity and the suppression of the H reflex while landing probably contribute to the development of the negative stiffness and change the muscles from a spring to a damping unit.

INTRODUCTION

The aim of the study reported here was to investigate how the central nervous system controls the intrinsic mechanical properties of muscles during voluntary movement. Different types of hopping and landing tasks, requiring either spring-like or damping properties of the muscles, were used as convenient models for the study of voluntary motor control in natural environments.

Skeletal muscles have spring-like properties and muscle stiffness influences the ability of muscles to absorb, store and release energy imposed by an impact. High muscle stiffness and ideal spring-like properties of the muscles would make it impossible to absorb an impact and stay on the ground after landing from a downward jump. Therefore during landing a special mechanism must make it possible to contract the muscles and at the same time keep the muscle stiffness low. During hopping spring-like properties of the muscles would be ideal and economical for maintenance of the activity.

Reflexes elicited from muscle spindles and tendon organs are believed to play an important role in adjustments to external disturbances. It is not known exactly how and when they operate during voluntary movement and there are several theories about their function. The muscle spindle could assist in the control of muscle length (Matthews, 1972; Marsden, Merton & Morton, 1976) and the tendon organ in the control of muscle force or they may co-operate and modulate length and force (stiffness) at the same time (Houk & Rymer, 1981). Finally reflexes could be suppressed if not useful or not functional for the motor act (Dyhre-Poulsen & Laursen, 1984). The spinal reflexes improve muscle stiffness (Hoffer & Andreassen, 1981) and the stretch reflex therefore modulates the intrinsic, mechanical properties of the muscles.

The relation between length and force (stiffness) of the contracted muscle is not linear. This non-linear behaviour of the muscles has been thought to represent deficiencies in muscle performance which were partially compensated by motor servo actions (Houk & Rymer, 1981; Hoffer & Andreassen, 1981; Sinkjær, Toft, Andreassen & Hornemann, 1988). The non-linear behaviour could, however, be an advantage during certain types of movements, such as landing from a downward jump, where spring-like behaviour of the muscles would be convenient. Therefore, if stretch reflexes increase muscle stiffness, stretch reflexes should be inhibited while landing.

In humans intentionally falling forward and landing on their arms, EMG bursts with a timing compatible with spinal stretch reflexes were discerned in the EMG pattern of the triceps brachii muscle just after touch down (Dietz & Noth, 1978; Dietz, Noth & Schmidtbleicher, 1981). Contrary results were found in monkeys where programmed rather than reflex activity was elicited after landing on their arms from a downward jump (Laursen, Dyhre-Poulsen, Djørup & Jahnsen, 1978; Dyhre-Poulsen, Laursen, Jahnsen & Djørup, 1980). These results from monkeys have been confirmed by McKinley, Smith & Gregor (1983) in cats. When landing from a downward jump monkeys keep the muscle stiffness low (Dyhre-Poulsen & Laursen, 1984), presumably to avoid bouncing.

In an attempt to analyse the landing mechanism further with special emphasis on the control of stretch reflexes and muscle stiffness during energy absorption, we have extended our earlier studies on monkeys to humans. It is technically difficult, if not impossible, to monitor and control a mechanical stimulus during vigorous movements and instead the Hoffmann (H) reflex was used as a measure of the excitability of the central component of the stretch reflex arc. The stretch reflex and the H reflex are different, but in the present study it was assumed that substantial changes in the H reflex excitability would also imply parallel changes in the excitability of the stretch reflex.

Changes in the size of the H reflex are normally believed to reflect the efficacy of the transmission from the Ia afferents to the α-motoneurones. The magnitude of the H reflex is modulated by preceding, on-going or future voluntary movement and by nearly any sensory input or change of state, often in an unpredictable way (Schieppati, 1987). Normally the reflex is increased as a function of the voluntary contraction in the muscle where the reflex is elicited but contractions in other muscles and cutaneous and/or other afferent input to the α-motoneurones may change the amplitude of the H reflex. The H reflex can even be smaller during voluntary contraction than during the control situation at rest (Schieppati & Crenna, 1984). The amount of facilitation or inhibition of the H-reflex depends on the preceding voluntary (Romanò & Schieppati, 1987; Gregory, Mark, Morgan, Patak, Polus & Proske, 1990) and also on electrically elicited motor activities (Crone & Nielsen, 1989). The neural mechanism by which the modulation of the H reflex is brought about is difficult to determine. The most probable mechanism for depression of the H reflex is presynaptic inhibition (Capaday & Stein, 1989). Changes in the combination of excitatory and inhibitory input to the α-motoneurones, changes in membrane conductance of the α-motoneurones and even bistable behaviour of the α-motoneurone are also possible mechanisms responsible for the modulation of the H reflex (Schieppati, 1987; Hounsgaard, Hultborn, Jespersen & Kiehn, 1988).

In the present study the biomechanics of landing and variations in the size of the H reflex were examined in humans during hopping and before and after landing from a downward jump. Some of the data have been presented in abstract form (Dyhre-Poulsen & Simonsen, 1991).

METHOD

Subjects and procedure

The experiments were carried out on three healthy good-to-excellent male volleyball players all of whom gave informed consent to the experimental procedures. They were aged 24–30 years, were 1·87–1·99 m high, had a weight of 84–97 kg and had received extensive daily training where both take-off and landing techniques were practiced.

The experimental procedure involved recording of EMG from leg muscles, measuring H reflexes and calculating muscle stiffness during movement in three situations:

(1) *Landing*. This involved jumping downward from a box 0·6 m high onto a force platform. The subjects were instructed to land naturally on both feet, then slowly return to standing position.

(2) *Drop jump*. This involved jumping downward from a box 0·6 m high onto a force platform, reverse the downward velocity as soon as possible and take off with maximal force.

(3) *Hopping*. This involved hopping on the force platform at the subject's preferred frequency, which proved to be about 2 Hz, on average.

The arms were held akimbo during hopping and jumping in order to avoid individual differences in jumping style and to simplify the calculation of the centre of mass during the movements. The subjects were instructed to perform the drop jumps as fast as possible without reducing the height of the following upward jump from the force platform. This instruction was given in order to avoid the subjects splitting the movement into two parts consisting of a landing and a take off with a short pause in between. The subjects were instructed not to lower their centre of mass by bending their knees before the take off from the 0·6 m box. This was necessary in order to obtain the same impact velocity at touch down in all jumps.

The excellent physical condition of the subjects made it feasible to record all jumping situations for a subject in one experimental session. In total a subject performed more than 200 landings, 200 drop jumps and 400 repeated hoppings in a session lasting about 5 h without reduction of maximal jumping height or any sign of fatigue.

In the landing session the muscles must first absorb the impact and then release the energy not as mechanical energy but let it dissipate as heat, so that the body is slowed to a halt. Ideally, hopping requires elastic behaviour of the muscles. In the drop-jump session the muscles may show mixed elements of elastic and/or impact-absorbing properties depending on the style and technique used by the subject (Bobbert, Huijing & van Ingen Schenau, 1987).

Force platform

The landing platform (AMTI OR6-5-1) multicomponent force platform) was 0·5 × 0·4 m with a smooth but hard surface. The platform measured the landing forces in three orthogonal dimensions and had a resonance frequency of about 500 Hz. The subjects were bare-footed. The ankle position was recorded with a Penny & Giles M-series twin-axis goniometer.

The electromyogram

Surface EMG electrodes (Medicotest Q-10-A pre-filled ECG electrodes) were placed 2 cm apart over the distal third of the soleus muscle about 16 cm above the calcaneus, over the anterior tibial muscle about 12 cm below the caput fibulae and over the most prominent part of the medial head of the gastrocnemius muscle. The electrodes were connected directly to small custom-built preamplifiers taped to the skin. The EMG signals were lead through wires to custom-built amplifiers with a frequency response of 20 Hz to 10 kHz. No observable cross-talk between EMG channels could be seen at 8 times the amplification used and cross-correlation between the raw soleus and gastrocnemius EMG was low and of the same magnitude as the cross-correlation between activity periods in the anterior tibial muscle and the soleus muscle. The fixed-wire set-up permitted the subjects to move freely and prevented recording of disturbing movement artifacts. Neither passive movement of the leg nor tapping the leg produced any visible artifact.

Cinematography

The whole movement was filmed at a rate of 500 frames/s using a Teledyne DBM45 film camera. The camera was placed 3·45 m from the force platform facing the volleyball player in profile as he landed. Reflective markers were glued over bony protuberances as indicated in Fig. 1. Touching the landing platform lit a diode that was used to synchronize the film to the force and EMG recordings.

The stimulus

The H reflex was evoked using a 10 mm diameter AgCl cathode in the popliteal fossa and a big 40 mm diameter anode placed over the patella. The EMG electrodes on the soleus muscle served to record the H reflex. Great care was taken to ensure that their placement produced selective recording of the M wave and the H reflex only from the soleus muscle. The placement of the recording electrodes and changes in muscle geometry influence the amplitude and shape of both the M wave and the H reflex (Gerilovsky, Tsvetinov & Trenkova, 1989). Therefore it was assured that passive movement of the ankle joint or light pressure applied to the cathode did not change the amplitude of the M wave and the H reflex. Large changes in ankle joint angle could cause minor changes in the shape of the M wave and the H reflex. However, the peak-to-peak amplitudes were unaffected. In some of the preliminary experiments both surface electrodes and intramuscular wire electrodes were used. As the wire electrodes produced discomfort during movement, and we found no difference in the results if the surface electrodes were positioned with care, we performed most of the experiments with surface electrodes only.

The stimuli were 1 ms square pulses delivered by a constant-voltage stimulator (DISA Ministim). The stimuli were delivered every 2 s in the hopping sessions. In the landing and the drop-jump sessions one stimulus was delivered in every jump, triggered by a photocell mounted 0·45 m above the platform. A variable delay dispersed the stimuli randomly over all the phases of the jumps.

Changes in the size of the H reflex reflect the changes in the excitability of the myotatic reflex arc provided the stimulus and therefore the in-going volley in the I a afferent fibres are of the same magnitude in each trial. During locomotion the electrodes move and the distance between the stimulus electrode and the nerve changes because of the large movements of the knee joint. Therefore the major problem is to monitor and control the effective stimulus strength. Using the M wave as a measure of the effective stimulus strength and repeating the experiments many times with several stimulus intensities it is possible to sample H reflexes with matching M waves during the different phases of the movement. This method requires many repeated stimuli (Capaday & Stein, 1987) and numerous jumps to extract enough reflexes with matching M waves of a certain amplitude. The subjects could simply not sustain such long-lasting experiments. We therefore used the method of Crenna & Frigo (1987) and defined a reference excitability level of the H reflex for each subject sitting comfortably in a chair with the knee bent about 165 deg. The reflex excitability is high in this situation. The recruitment curves of the H reflex and the M wave were recorded at the beginning and at the end of each experimental session by stimulating every 2 s and randomly changing the stimulus strength and plotting the amplitude of each H reflex against the size of the associated M wave (Fig. 2). A fourth-order polynomial function describing the relation between the size of the H reflexes and the M waves was fitted to the experimental data, stored in a computer, and later used as the reference excitability level. In this way it is not necessary to control the effective stimulus strength so rigorously. The effective stimulus strength varied in a predictable way throughout the locomotor cycle and the stimulus strength was therefore adjusted during the locomotor cycle so that the effective stimulus strength elicited an M wave with an amplitude of 15–35% of the maximal M wave during all phases of the movement. By adjusting the stimulus strength we could control the size of the M wave so well that more than half of the M waves fulfilled our criteria. We used the falling part of the reference excitability curve where different sensitivity of inhibition or facilitation might bias the estimated excitability changes (Meinck, 1980; Crenna & Frigo, 1987). It was necessary to use rather large M waves to minimize the error caused by the background EMG during certain phases of the locomotor cycle. The use of relatively large stimulus strength and large M waves also confines the effects measured to the smaller α-motoneurones, those not involved in the formation of the M wave. However, the shape of the H reflex excitability curve recorded during movement was not changed if we changed the acceptance criteria and used either the lower end of the reference excitability curve with the small M waves or the higher end with the larger M waves.

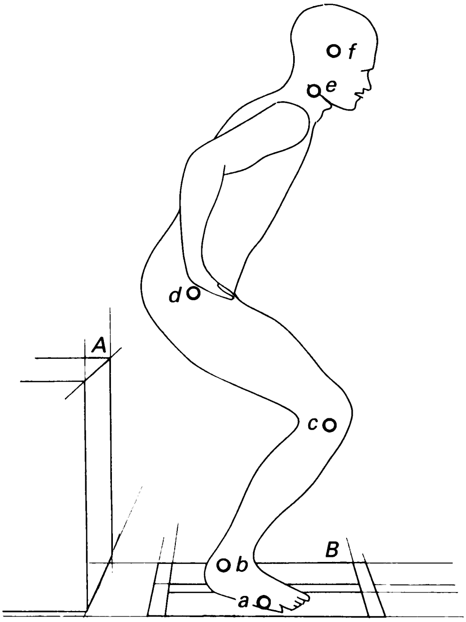

Fig. 1. The experimental set-up consisting of a take-off platform (*A*) and a landing platform (*B*). The points marked *a*–*f* on the subject were digitized from each frame of the film and later connected by lines depicting the movement of the body segments above the recordings in Fig. 6.

The H reflex and the M wave were recorded while the muscles were active and the underlying

EMG therefore interfered with the measurements of their amplitudes. Adding EMG on top of the M wave and the H reflex would tend to determine a relatively higher H reflex during EMG activity than during rest. Using the area of the H reflex and M wave instead of their amplitude might diminish this possible error but it did not change the shape of the H reflex excitability curve recorded during movement.

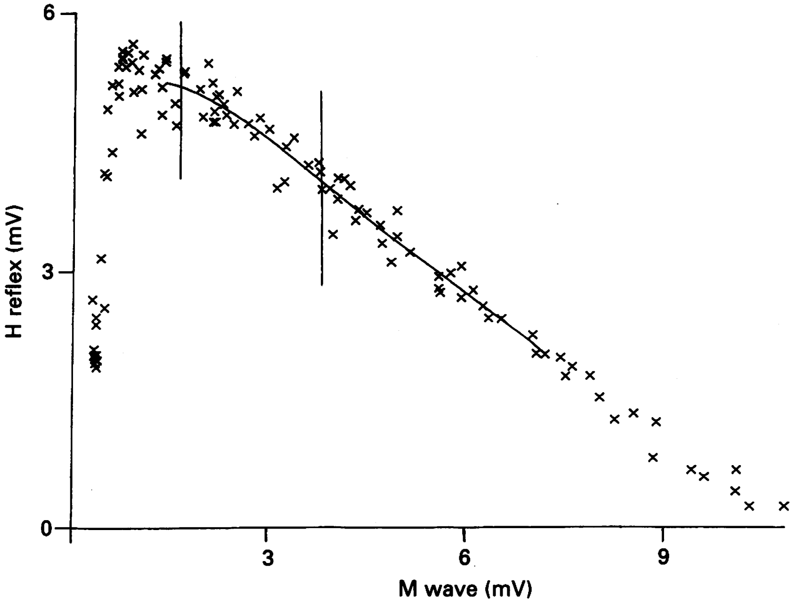

Fig. 2. A reference excitability curve recorded while the subject was sitting comfortably in a chair. The stimulus amplitude was varied randomly and for each stimulus the amplitude of the H reflex was plotted against the amplitude of the M wave. A fourth-order polynomium (continuous line) was fitted to the experimental data and stored in a computer. For every M wave recorded during the movements, the polynomium was used to calculate the relation between the recorded and the expected amplitude of the H reflex. Only stimuli eliciting M waves with an amplitude between 15 and 35% (vertical lines) of the maximal M wave were used. The excitability of the H reflex is usually high when sitting relaxed in a chair.

Data analysis

The experiments were controlled by a program written in ASYST and running on a fast personal AT computer. During the experiment the EMG, the landing forces and the ankle position were sampled at 20 kHz. The amplitude of the M wave and the H reflex was measured and the size of the H reflex during movement in percentage of the H reflex at rest was calculated from the amplitude of the M wave and the reference excitability level polynomium. This relative size of the H reflex was plotted against the phase of the locomotor cycle and displayed together with the M wave and the H reflex on the computer screen.

The signals were stored on tape (TEAC XR-510), and later A–D converted, rectified and averaged by the computer. The parts of the EMG and force recordings starting just before the stimulus artifact and lasting 200 ms were not included in the averaging. This was necessary because the amplitudes of the stimulus artifacts, the M waves and the H reflexes were large compared to the amplitude of the EMG. The relative size of all 150 H reflexes from one session was plotted against the phase of the locomotor cycle and depicted on top of the averaged EMG and force recordings obtained from twenty-four representative task repetitions taken from the middle of the same session. The onset and timing of the EMG peaks were estimated by visual inspection of the averaged EMG recordings.

In the movement analysis the body was first divided into four rigid segments connected by simple joints with one axis of rotation and one degree of freedom. The film was projected frame by frame on a digitizer and the co-ordinates of the reflective markers were used by the computer to reconstruct the movements of the body segments. The data were digitally smoothed (Butterworth fourth-order low-pass filter with a cut-off frequency of 8 Hz) to minimize measurement inaccuracies from film digitation. Then from anthropometric data (Dempster, 1955; Frigo & Pedotti, 1978) and from the force recordings from the landing platform the whole movement, the instantaneous angular velocities of the involved joints and the muscle lengths were calculated. The net muscle moment about the ankle joint was calculated by inverse dynamics (Elftman, 1939; Winter, 1979).

Calculation of muscle stiffness

Calculation of muscle stiffness requires estimation of both muscle length and muscle force for the individual muscles. The length can be calculated as a function of both the angle of the ankle joint and the knee joint, but the force produced by the different parts of the triceps surae cannot be measured easily. It was therefore not possible to calculate the exact muscle stiffness of the individual parts of the triceps surae muscle. Available anthropometric data show that the physiological cross-sectional area of the soleus muscle in the human is about three times larger than the summed cross-sectional areas of the lateral and the medial head of the gastrocnemius muscle (Friedrich & Brand, 1990). During landing the absolute stretch of the gastrocnemius muscle is reduced by flexion of the knee joint, while the soleus muscle is influenced only by dorsiflexion of the ankle joint. It was therefore assumed that the force generated about the ankle joint was due primarily to the eccentric contraction of the soleus muscle.

The combined dynamic stiffness of the muscles acting about the ankle joint was finally calculated as increment in moment divided by increment in ankle rotation during the particular task disregarding the movements in the knee joint. This is the functional property of estimated muscle stiffness acting during the particular task. Total body stiffness was calculated from the force platform signals as described by M. Voigt, E. B. Simonsen & P. Dyhre-Poulsen (in preparation). Briefly, in the landing experiments the touch-down impulse was calculated by backward integration of the force produced by the braking of the body mass. When the touch-down impulse was found, the touch-down velocity was calculated and the displacement of the body centre of mass during landing was found by double integration of the vertical force. During hopping the touch-down velocity was calculated from the duration of the flight phase. Total body stiffness was then calculated as increment in force divided by increment in displacement of the body centre of mass.

RESULTS

The landing movements

The kinetic analysis of jumping and hopping showed an extraordinary degree of reproducibility within subjects. They could stop and rest for a while and then resume the task with the same jumping height or frequency. This was not the case in preliminary experiments with untrained subjects.

Landing

The effective jumping height calculated from the touch-down velocity was about 0·57 m. The maximal moment was about 250 N m (Fig. 6*A*) and the velocity in the ankle joint reached 750 deg s^{-1}, corresponding to a shortening velocity in the anterior tibial muscle of 0·7 m s^{-1}. The vertical ground reaction force had a steep onset with an inflexion on the rising phase (Fig. 3); it reached about 4500 N and declined slowly with one or two minor bulges before the heel was lowered smoothly to the platform.

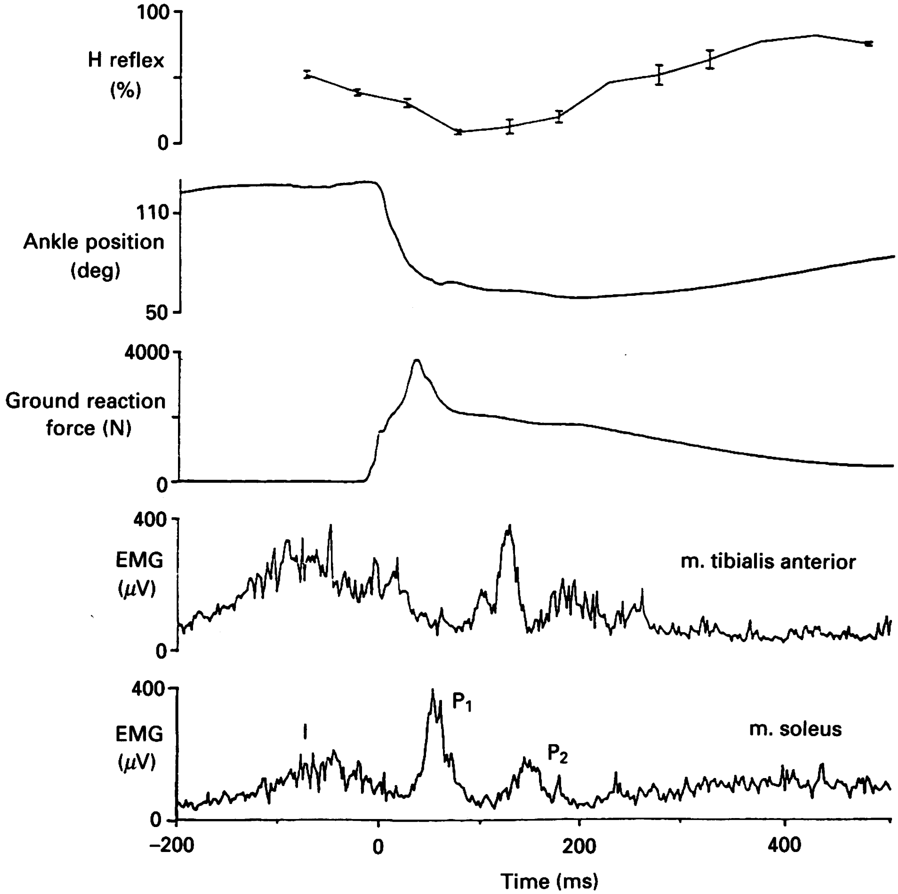

Fig. 3. Landing from a downward jump. The H reflex was elicited randomly during the downward jump. Each point represents the mean within a time period of 50 ms of the H reflexes in percentage of their resting value. The total number of H reflexes was 150. Vertical bars are standard error of the mean. The amplitude of the H reflex was very low at touch down, but recovered after landing. The H reflex during movement was generally lower than the H reflex recorded at rest. The ankle position recorded with a goniometer illustrates the fast stretch of the soleus muscle. The vertical ground reaction force had an inflexion on the rising phase when the short-range stiffness of the ankle plantar flexors was exceeded and the cross-bridges probably broken. The rectified EMG from the anterior tibial muscle and from the soleus muscle showed a programmed preparatory co-contraction in flexors and extensors (I) that declined before touch down. The two peaks after landing (P_1 and P_2) in the soleus muscle alternated with the activity in the anterior tibial muscle. The amplitude of the soleus EMG was lower than the EMG recorded during maximal voluntary contraction. Each record was rectified and averaged from twenty-four jumps taken from the middle of same session as the H reflexes on top. The part of each record containing the stimulus and 200 ms thereafter was not included in the averaging. The records are lined up with touch down (0 ms) as reference.

Hopping

The hopping frequency was about 1·9 Hz and the height about 0·10 m. The centre of mass was moved about 0·30 m up and down during the hopping. The maximal moment was about 500 N m (Fig. 6*B*) and the velocity in the ankle joint reached

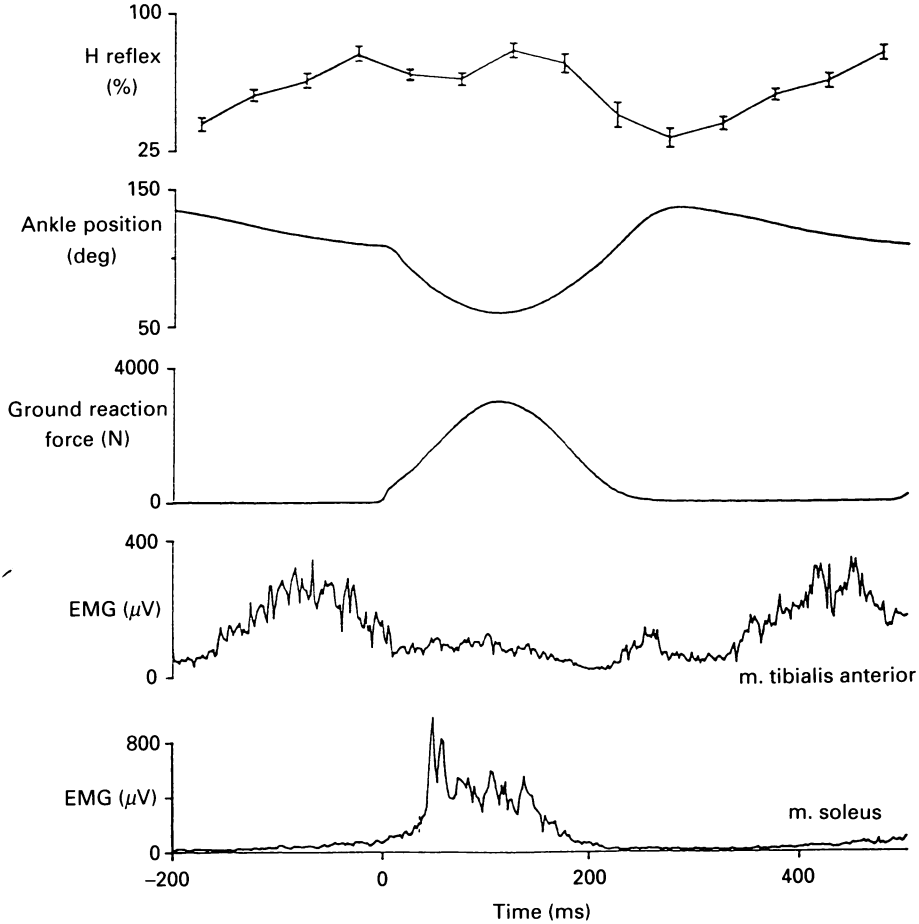

Fig. 4. Hopping. The H reflex was low in the flight phase, but increase before touch down (0 ms) and remained high during the stance phase. The H reflex during movement was generally lower than the H reflex recorded at rest. The ankle position was recorded with a goniometer. The vertical ground reaction force was smooth without inflexions. There was a preparatory contraction in the anterior tibial muscle, low activity during the stance phase and a small peak just after take off. In the soleus muscle a feeble activity counterbalanced the anterior tibial activity at touch down. A sharp peak, probably caused by a stretch reflex, followed about 45 ms after the touch down, then a sustained period of activity lasted until take off. The amplitude of the soleus EMG during take off was as high as the soleus EMG recorded during maximal voluntary contraction. Each record was rectified and averaged from twenty-four jumps. The records are lined up with touch down as reference.

450 deg s^{-1}, corresponding to a shortening velocity in the anterior tibial muscle of 0·4 m s^{-1}. The vertical ground reaction force (Fig. 4) had a maximum of 4500 N and a very smooth bell shape, occasionally with an inflexion just after impact.

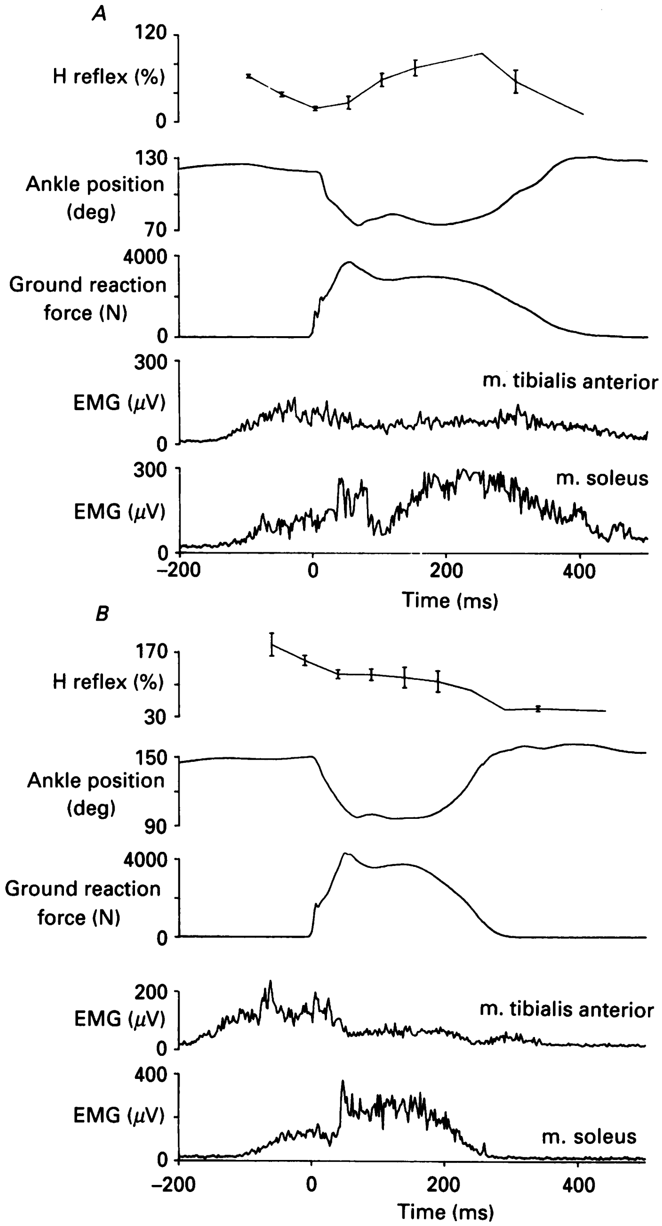

Fig. 5. Drop jumps. *A*, landing type of drop jump. The H reflex declined and was very low at touch down but recovered during the stance phase. The ankle position indicated a fast stretch of the soleus muscle. The vertical ground reaction force had inflexions on the rising phase, probably indicating loss of strain energy. The stance phase lasted more than 400 ms. The initial part of the EMG in the anterior tibial and in the soleus muscle showed segmented activity with a pattern resembling landing from a downward jump. About 100 ms after touch down the take-off EMG dominated. *B*, hopping type of drop jump. The H reflex was high before and during touch down and remained high until lift off. The vertical ground reaction force had inflexions on the rising phase, indicating loss of strain energy. The stance phase lasted about 250 ms. The EMG in the anterior tibial and in the soleus muscle showed activity with an unsegmented hopping pattern as in Fig. 4.

The electromyograms

Landing

The electrical activity in the soleus muscle started, judged by visual inspection of the averaged recordings, about 150 ms before touch down and increased slowly (Fig. 3). The initial burst (I) in the soleus muscle ended just after touch down. A second and more intense burst (P_1) started about 45 ms after the touch down, lasted for 50 ms and was followed by a smaller burst (P_2). In some of the raw EMG recordings additional bursts, smaller in amplitude, could be discerned, but they were less constant and tended to fade away in the averaged tracings.

The EMG activity in the medial head of the gastrocnemius muscle looked much like the activity in the soleus muscle; it began with an initial burst about 160 ms before touch down and continued with one or two peaks after touch down.

The electrical activity in the anterior tibial muscle started about 170 ms before touch down, increased slowly, peaked about 50 ms before touch down and then declined slowly. After touch down followed two or three dwindling peaks with intervening pauses. Peaks in the anterior tibial EMG coincided with pauses in the soleus EMG. This reciprocal pattern of activation was seen most clearly in the raw recordings as the averaging tended to obscure the later peaks and pauses. The EMG pattern was the same when landing from only 30 cm, but the amplitude of all the peaks and the averaged EMG were smaller, so the subjects adapted their motor programme to the jumping height.

Hopping

The electrical activity in the soleus muscle and in the anterior tibial muscle showed a different pattern during hopping (Fig. 4) than during landing. The activity in the soleus muscle was low during the flight phase. It started to increase very slowly after touch down and then a high peak began about 45 ms after touch down. The activity remained high for about 100 ms, then slowly declined and ended about 50 ms before take off. During the flight phase there was no activity in the soleus muscle. The EMG activity in the anterior tibial muscle showed the opposite pattern. It was low during the stance phase, increased during the flight phase, but ended just before touch down. When instructed to increase the hopping height the amplitude of the EMG increased. The activity in the gastrocnemius muscle showed the same pattern as found in the soleus muscle during the stance phase. During the flight phase a preparatory burst was present in the anterior tibial muscle.

Drop jump

The EMG pattern during the drop jumping was reproducible within subjects but varied among subjects. In one subject (Fig. 5*A*) the EMG pattern resembled the landing type of EMG pattern with a peak and a pause shortly after touch down. The later part of the pattern was disturbed by the high soleus activity preceding take off. The stance phase in this subject lasted about 400 ms and he probably performed a landing followed by a take off in two steps in spite of the instruction given (counter movement type of drop jump, Bobbert *et al.* 1987). In another subject (Fig. 5*B*) the EMG pattern closely resembled the pattern found in hopping. The soleus activity was low until 45 ms after landing where a peak was followed by a plateau lasting until the beginning of the plantar flexion for take off. The stance phase was short, about 250 ms. The short stance phase and the hopping type of EMG suggest that he performed a bouncing type of drop jump (Bobbert *et al.* 1987).

The subject with the hopping type of EMG had a short stance phase and could probably maintain high muscular activity, store most of the impact energy and release it as mechanical energy during take off. If the stance phase is too long this is probably not possible or too energy consuming.

The EMG activity in the gastrocnemius followed the pattern of the soleus muscle in all situations and for all subjects.

The H reflex

The amplitude of the H reflex during movements was generally lower than the reflex measured at rest where the H reflex excitability usually is high. The excitability of the H reflex did not follow the changes in EMG amplitude of the soleus muscle nor was it controlled by antagonist muscle activity in the anterior tibial muscle. It showed a marked and distinctly different modulation pattern during the movement in the three situations.

Landing

In the landings the H reflex excitability was slowly declining before touch down, it was low at touch down and nearly absent 50 ms later (Fig. 3). The H reflex was therefore strongly inhibited while landing from a downward jump. The inhibition started more than 100 ms before touch down and the inhibition of the H reflex must therefore be programmed and a part of a motor programme controlling the landing. After landing the excitability of the H reflex slowly returned towards the reference excitability level.

Hopping

In the hopping task the H reflex excitability (Fig. 4) was very low at take off, low in the flight phase, increased just before touch down, remained relatively high during the stance phase but decreased just before take off as recently reported by Moritani, Oddsson & Thorstensson (1990). The modulation of the H reflex did not reflect the activity in the soleus muscle and/or antagonist EMG activity. It was high before touch down when the activity in the soleus muscle was very low and the activity in the antagonist muscle was high. Therefore the high H reflex excitability at the time of impact probably indicates that the EMG peak about 45 ms after touch down was elicited by a stretch reflex on top of a relatively high motoneurone excitability.

Drop jump

In the subject with the long stance phase and the landing type of EMG pattern the H reflex excitability was low at the time of touch down (Fig. 5*A*). In the subject with the short stance phase and the hopping type of EMG pattern (Fig. 5*B*) the H reflex excitability was unusually high before touch down and was high during most of the stance phase. Otherwise this subject had H reflex excitabilities that never exceeded 100%. Thus the EMG modulation pattern and the H reflex excitability pattern co-varied during drop jumps and they were adapted to the strategy used by the subjects.

Muscle stiffness

After touch down the triceps surae developed high forces as it was stretched.

Landing

The calculated dynamic stiffness in the ankle joint first increased for 10 ms (Fig. 6*A*) then decreased and finally became negative for the remainder of the impact.

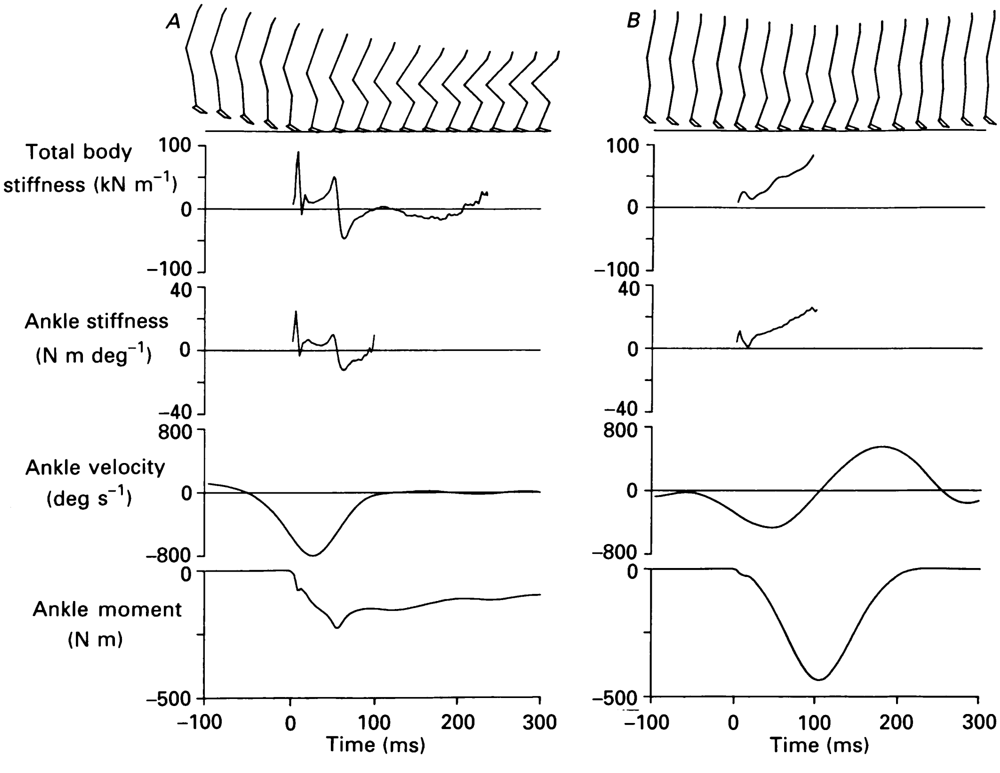

Fig. 6. *A*, landing. On top, stick diagram of the landing. The total body stiffness during landing looked like the stiffness at the ankle joint calculated from the ankle moment and the ankle joint angle. The stiffness at impact was high, probably due to the short-range stiffness. When the short-range stiffness is exceeded the breaking of cross-bridges could permit the stiffness to decrease and become negative due to the high rate of muscle lengthening. The velocity of the movement in the ankle joint was calculated from the film points marked *a*, *b* and *c* in Fig. 1. Dorsiflexion is negative. The ankle moment in both legs was calculated from the film and the ground reaction forces. The curve had a sharp rise at touch down and an inflexion on the rising phase. Increased moment is negative due to convention. *B*, hopping. On top, stick diagram of the hopping. Most of the movement took place at the ankle joint. The total body stiffness and the ankle stiffness had the same shape indicating that most of the braking took place at the ankle joint. The stiffness at impact was high probably due to some preparatory EMG activity and the short-range stiffness of the active cross-bridges. The stiffness decreased until the activity in the soleus muscle increased and induced high muscular stiffness. The ankle moment in both legs was calculated from the film and the ground reaction forces. The curve had a smooth even bell shape with a small bulge just after touch down.

Negative stiffness implies that mechanical energy was lost and that there was little or no elastic energy stored in the muscle or tendons when the landing was completed.

Hopping

The calculated dynamic stiffness first increased (Fig. 6*B*) then declined somewhat, but increased again while the muscles were stretched. The muscles and the tendons acted as springs and the high stiffness probably improved efficiency.

The total body stiffness

Total body stiffness was estimated from the force recordings and the kinetic energy. The time course of total body stiffness resembled the time course of the stiffness in the ankle joint during the dorsal flexion. When landing from the downward jump total body stiffness was very low or negative when the ankle stiffness was negative. The minor discrepancies between the two curves are probably due to movement in the knee and hip joints.

During hopping total body stiffness was positive during the ankle dorsiflexion and followed the development of the stiffness in the ankle joint. Thus most of the braking of the body took place at the ankle joint. The movements in the knee and hip joints were small.

DISCUSSION

The results elucidate the different mechanisms the central nervous system uses to adjust the mechanical properties of the muscles to the different requirements appropriate for life. It is obvious that the classical view of active muscles acting as springs obeying the well-known static length–tension relationship obtained in isolated muscles cannot function uniquely during dynamic movement. The dynamic behaviour of the motor system was very different from the static behaviour and furthermore the dynamic behaviour was adapted to the requirements of the motor task.

The experiments revealed several striking features. First the skilled volleyball players were able to repeat the same movement in an automatic reproducible way so that the electromyographic pattern, the force recordings and the joint movements looked the same in every recording for a given subject for a given motor task. Secondly, both the electromyographic pattern and the excitability of the H reflex were clearly adapted to the different motor tasks. Thirdly, the calculated stiffness in the ankle joint was also adjusted to the task; it was always positive just after touch down, but showed negative peaks when shock absorption was requested whereas it was continuously positive when elastic behaviour of the muscles was desirable.

When landing from a downward jump, braking force based on the static length–tension relation would be far from ideal. The braking force at impact would be low and increase steadily during the landing and at the end a large force would remain to be counterbalanced by the antagonist. The dynamic length–tension relation we found with the initial high stiffness at impact shifting to negative stiffness and the actual decrease in force at the end of the landing may be attributed to the high speed of the movement. In the landing task the soleus muscle–tendon complex was stretched 0·04 m and the lengthening velocity exceeded 0·7 m s^{-1}. Probably the initial sharp rise in vertical ground reaction force and high positive stiffness includes the short-range stiffness (Rack & Westbury, 1974), but as the elongation proceeds at high velocity the cross-bridges are broken and the tension and stiffness decline (Dyhre-Poulsen & Laursen, 1984). The decrease in stiffness was probably not due to antagonist activity as the imposed shortening velocity of the anterior tibial muscle exceeded 0·7 m s^{-1} where any force production would be minimal, nor was it due to a decrease in the overall agonist EMG activity. At the end of the movement only a small amount of tension would remain to be counterbalanced by the antagonists. The momentum of the body was probably transformed from strain to heat in the muscle during the stretch.

Negative muscle stiffness has been reported when submaximally contracted muscles were stretched at high velocity (Joyce, Rack & Westbury, 1969; Rack, 1981). They found that the stiffness, when the muscle was stretched by a muscle puller, depended in a complex manner on the stimulus frequency, the initial length and the velocity of the stretch. The maximal ankle moment (500 N m, both legs) and the maximal stiffness at the ankle joint (25 N m deg^{-1}) found during the landing and hopping far exceed the values reported from laboratory experiments (Sinkjær, 1988) where the lengthening velocity and range were lower than naturally occurring physiological values.

The EMG pattern found in the soleus and the anterior tibial muscle during landing looked like the programmed EMG pattern found in the elbow muscles in monkeys landing from a downward jump (Dyhre-Poulsen & Laursen, 1984). The initial EMG activity in the anterior tibial and in the soleus muscle started before touch down. After touch down the EMG activity was transformed to an alternating pattern of bursts and pauses. The peaks P_1 and P_2 were present while the excitability of the H reflex was low, therefore they were probably not elicited by reflexes. However, the timing of the peaks was about the same as the timing of the EMG peaks elicited by rotating the ankle joint with a torque motor (Toft, Sinkjær & Andreassen, 1989). Those peaks normally labelled M_1 and M_2 (Lee & Tatton, 1975) are believed to be of reflex origin, but some evidence supports the idea that the singular later peaks are not due to reflexes, but part of a motor programme elicited as a whole by the stretch of the muscle (Ghez & Shinoda, 1978). The low H reflex excitability at the time of impact makes it probable that the EMG peaks (P_1 and P_2) after touch down are part of a motor programme and not elicited by stretch reflexes. This is probably the same type of central motor programme as the programme controlling the EMG activity in cats and monkeys jumping downward (McKinley, Smith & Gregor, 1983; Dyhre-Poulsen & Laursen, 1984).

The amplitude of the EMG peaks was low, only about 50% of maximal voluntary EMG amplitude, so the muscles were far from maximally activated during landing from the 0·6 m high jump. High activation frequency of the motor units makes the muscle stiffer, therefore a problem arises when both high-force and non-spring-like properties are required as when landing. The orderly recruitment scheme of motor units used for isometric or shortening contractions (Hennemann, Sojmen & Carpenter, 1965) indicates high activation frequency of all small motor units while the recently activated larger units are submaximally activated. When landing all active motor units could be submaximally activated in order to produce low stiffness

(Joyce *et al.* 1969) and a method for lowering the α-motoneurone firing frequency could be to let a motor programme directly inhibit all α-motoneurones for short periods of time, that is produce a segmented EMG. The different peaks in the EMG probably were produced by different motor units in the different peaks (Bawa & Tatton, 1979) and that may explain the relatively low amplitude of the peaks compared to the amplitude during maximal voluntary contraction. Furthermore, if it is possible selectively to recruit high-threshold (large) motor units during lengthening contractions (Nardone, Romanò & Schieppati, 1989), then the maximal activation frequency of smaller motor units could be kept low while large forces are produced and this could make the muscle behave as a damping unit. If the mechanical behaviour of the muscles is critically dependent on the activation pattern of the muscle fibres it would be an advantage to suppress external inputs and let the central nervous system take control of the firing of the α-motoneurones. This suppression of the external input could be due to presynaptic inhibition of the afferents (Capaday & Stein, 1989).

When hopping, elastic behaviour of the muscles would be ideal just as in hopping kangaroos (Morgan, Proske & Warren, 1978). The impact energy is stored in the muscles and tendons and released during the take off (Asmussen & Bonde-Petersen, 1974). Therefore the mechanical efficiency of hopping is very high compared to other motor tasks (Thys, Cavagna & Margaria, 1975).

The EMG pattern elicited while hopping looked quite different from the landing EMG. There was no or very little preparatory activity in the soleus muscle and the EMG started abruptly with a high peak just at the expected time for a stretch reflex. The EMG continued uninterrupted for a period of about 100 ms until take off. Probably the peak at the beginning of the soleus activity after touch down was elicited by stretch reflexes as in blindfolded humans landing on their arms (Dietz *et al.* 1981). The H reflex showed high excitability at the time of touch down and impulses from the Ia afferents could therefore add a reflex response on top of the voluntary EMG activity or produce a peak by synchronizing the α-motoneurones in the already active soleus muscle. The presence of positive feedback from the muscle spindles while hopping presumably increased muscle stiffness during the stance phase and facilitated the storage of strain energy in muscles and tendons while hopping.

In conclusion we suggest that the segmented EMG pattern found during voluntary landing and when a muscle is suddenly stretched probably changes the muscle from a spring to a damping unit. We believe that the negative muscle stiffness is a property of decisive functional importance in motor control and that stiffness is one of the most important regulated properties of muscles. The segmented EMG pattern is probably produced by a central programme and not or very little influenced by afferent input as the programme also inhibits the stretch reflex as measured by the H reflex.

This work was supported by grants from the Danish Research Council for Sports, the Danish Elite Sport Association and the Danish Research Academy.

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