

The purpose of the present study was to establish the relationship between muscle architecture and H-reflex recordings in quadriceps femoris muscle. H-reflexes were elicited in human quadriceps femoris muscle over a broad area of skin to document the shape and amplitude of the H-potentials. This, in combination with recording monopolar and bipolar H-potentials, was performed to determine the location and method for measuring maximum-amplitude H-reflexes. The influence of neural and peripheral factors on the H-potential during passive length changes was studied by comparing the amplitude of H-potentials to motor unit action potentials. Monopolar recordings of the H-potential were found to be preferable to bipolar recordings because of the reproducibility of shape and easier distinction between the M- and H-potentials. The location for recording maximum H-potentials was in the distal one third of the quadriceps femoris muscle, over the border between vastus lateralis and rectus femoris. The inferred relationship between H-potential amplitude and reflex excitability must be made with caution in quadriceps femoris muscle because the amplitude of both the motor unit potential and H-potential change as a function of muscle length. © 1994 John Wiley & Sons, Inc.

Key words: motor unit • H-reflex • reflex excitability • quadriceps femoris • muscle architecture

MUSCLE & NERVE 17:581-592 1994

ASSOCIATION BETWEEN MUSCLE ARCHITECTURE AND QUADRICEPS FEMORIS H-REFLEX

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The Hoffmann (H-) reflex has been used as a valuable tool to test the human monosynaptic reflex excitability under normal and pathological conditions.^{22,23,32} The correct interpretation of any H-reflex data, however, requires reliable criteria for distinguishing between the effects of neural factors (segmental and supraspinal) from purely peripheral ones (muscle architecture, desynchronization of the potentials, volume conduction, passive changes in muscle fiber length, and diameter). Past attempts to delineate these factors

have included determining the influence of muscle fiber geometry and the peculiarities of the extracellular potential field on the shape and amplitude of the H-reflex potential.^{8-10,16} It was demonstrated that both monopolar and bipolar measurements of the H-reflex potentials (hereafter referred to as the monopolar and bipolar H-potential) and motor unit potentials were needed to provide a complete understanding of the reflex excitability underlying the H-reflex in quadriceps femoris. Whereas the amplitude of the H-potential can be influenced by neural and peripheral factors, the amplitude of the motor unit potential is subject only to peripheral factors. The comparison of these two potentials has implicated peripheral factors in the increase in the amplitude of the H-potential with passive shortening of soleus muscle in humans.¹⁰

Despite suggestions that the H-reflex can be obtained as easily from the quadriceps femoris muscle as from the triceps surae muscle,^{1,29} there is little information available documenting the optimal location for recording H-reflexes in quadriceps femoris muscle.³² One study has described a two-component bipolar H-potential from the rec-

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Acknowledgments: The authors thank Mr. Peter Worden for his invaluable technical assistance. The project was supported by grants from NIH (NS 07309 to the Motor Control Group, and NS 20544 to Drs. Enoka and Stuart) and from NSF (INT 8520863 to Dr. Stuart). Dr. S. Jayne Garland was a Fellow of the Ontario Ministry of Health, Health Research Personnel Development Program.

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Accepted for publication December 1, 1993.

CCC 0148-639X/94/060581-12
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tus femoris muscle.²⁵ This observation, however, may have been due to the difficulty associated with distinguishing between the direct short latency motor response (M-wave) and the later H-potential in bipolar recordings (see ref. 8). Resolution of this issue becomes particularly important if latencies are to be measured.

The purpose of the present study was to establish the relationship between muscle architecture and H-reflex recordings in quadriceps femoris muscle. There were three specific aims: (1) to determine the location that yields the largest peak-to-peak H-reflex amplitude by documenting the shape and the amplitude of the H-potentials measured over a broad area of skin above the quadriceps femoris muscle; (2) to compare the monopolar and bipolar measurements of the H-potential; and (3) to compare the amplitude of the monopolar H-potentials with the motor unit action potentials to delineate the influence of neural and peripheral factors on the H-potential during passive length changes of quadriceps femoris muscle. A preliminary report on this work has appeared in abstract form.¹¹

METHODS

Subjects. Experiments were carried out on 14 healthy adult volunteers, all of whom gave informed consent to participate in this investigation. It was not possible to evoke the H-reflex in quadriceps femoris muscle without either large M-responses or unavoidable activation of the sartorius muscle in 5 of these subjects and consequently these subjects were excluded from the study.

H-Reflex Testing. H-reflexes were elicited by surface cathodal stimulation (a single rectangular shock of 1-ms duration delivered at a rate of once every 5 s) delivered to the femoral nerve just below the inguinal ligament. It was not possible to distinguish the branches of the femoral nerve to the different components of quadriceps femoris. The pulse from the femoral artery was used as a landmark for positioning the cathode (1.0 cm²), denoted by an open circle (C) in Figure 1A. A large stimulus artifact, commonly found to accompany monopolar measurements of the H-reflex, was reduced using a pair of anodes according to the method proposed by Gerilovsky et al.^{9,10} The location of the anodes (each 8.0 cm²; AS₁ and AS₂ in Fig. 1B) was determined empirically. They were placed in the region of the greater trochanter such that on separate application of each anode, the stimulus artifact accompanying the H-potential

had approximately the same shape and amplitude but opposite polarity. When the two anodes were then short-circuited, the subsequent artifact was significantly reduced (Fig. 1C). Adjustment of the anodes was needed at each location of the recording electrodes. While documenting the H-potentials over a broad area of the quadriceps femoris muscle, continuous adjustment of the anodes was not appropriate. Therefore, the appearance of a stimulus artifact in some measurements was unavoidable.

Monopolar H-potentials were recorded with a multielectrode that had 19 poles, each with a small leading-off area of 1 mm² (Fig. 1D). The interpole distance along the longitudinal axis was 1.0 cm (poles 1–7) and 0.5 cm along the transverse axes (poles 8–13, 14–19). It should be emphasized that the term “monopolar H-potentials” is used only for convenience because they were actually bipolar measurements in which the reference electrode was located at such a distance from the multielectrode that the volume conducted potentials were comparable to the noise level (see ref. 16). The reference electrodes had a leading-off area of 2.0 cm² and were placed on the knee of the contralateral leg. Bipolar H-potentials were derived offline by subtracting between vertically aligned poles with interelectrode distances of 2.0 cm.

Additional monopolar H-potentials were recorded from an electrode (1 mm²) fixed over vastus lateralis during the measurements with the multielectrode. These H-potentials served as a control to verify the stability of the H-potentials at a fixed point so that the changes in the shape and amplitude of the H-potentials could be interpreted as due to differences in muscle geometry rather than changes in central excitability.

Motor Unit Potentials. Monopolar surface measurements of single motor unit potentials from quadriceps femoris muscle were obtained using spike-triggered averaging techniques.²⁸ Surface measurements were necessary to uncover the influence of peripheral factors (i.e., volume conduction, muscle fiber geometry) on the motor unit potential. This allowed for the proper comparison between the H-potential and the motor unit potential. The motor unit potentials were recorded during sustained low-level voluntary contraction and were selectively identified with an intramuscular needle or fine-wire electrode. The electrodes were inserted in the middle of the respective muscle bellies to a depth of about 2–3 cm. The intramuscular motor unit potentials were used as reference

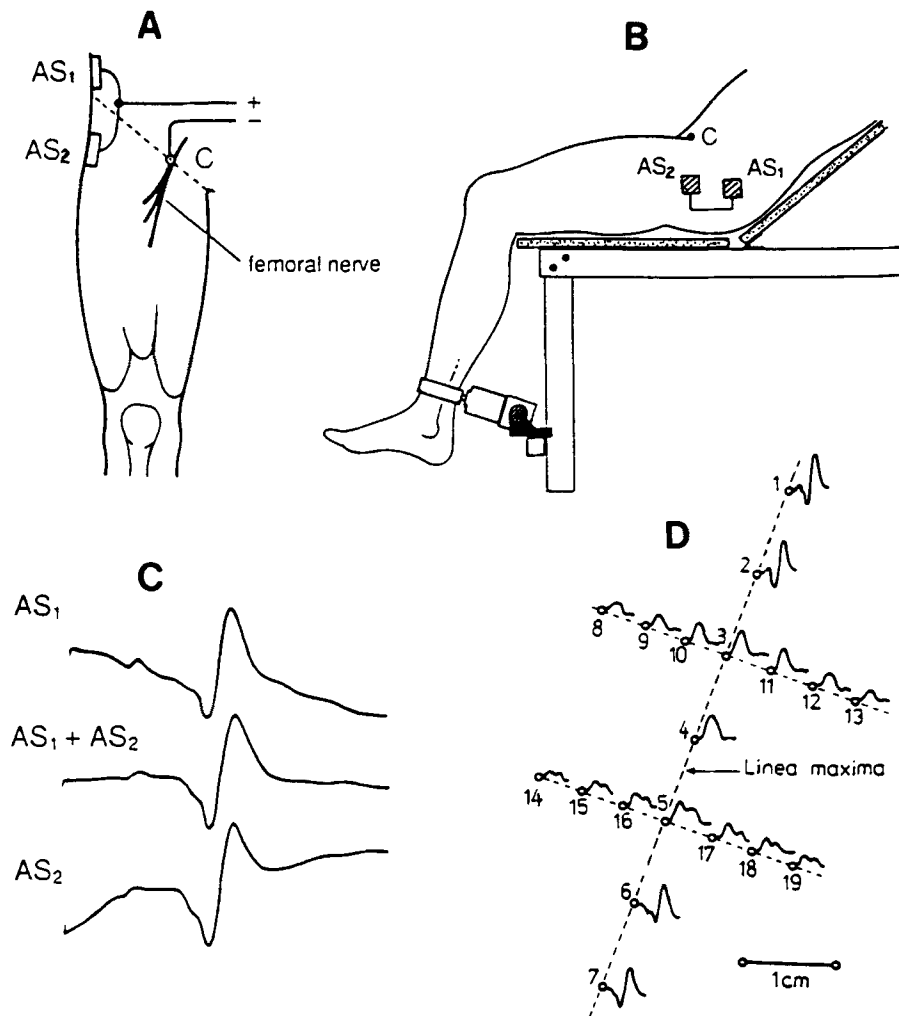


FIGURE 1. Electrode configuration and subject position for measuring H- and motor unit potentials. **(A)** H-potentials were elicited in quadriceps femoris by cathodal stimulation and a pair of anodes. The two anodes (AS₁ and AS₂) were placed over the greater trochanter and the cathode (C) was placed over the femoral nerve in the inguinal crease. **(B)** The subject lay in a semireclined supine position with the leg strapped to a force transducer at the ankle. **(C)** The use of a pair of anodes to minimize the stimulus artifact. The upper trace is the potential measure when the anode was AS₁, lower trace corresponds to an anode of AS₂, and the middle trace represents the potential obtained when AS₁ and AS₂ were short-circuited. **(D)** Schematic presentation of motor unit potentials obtained from the rectus femoris muscle as recorded with a 19-pole multielectrode. The multielectrode was oriented to identify the linea maxima, which is defined as the line containing the motor unit potentials with the greatest peak-to-peak amplitude.

events with which to average the potentials as measured by surface electrodes. The surface-measured motor unit potentials were derived online from an average of 128 or 256 sweeps. The common reference electrode (2.0 cm²) was placed on the ipsilateral knee.

The shape and amplitude of 21 motor units from four subjects (8 motor units from vastus lateralis, 9 motor units from rectus femoris, 4 motor units from vastus medialis) were studied to determine the location of the "linea maxima" (Fig. 1D), which is defined as the line along which the motor

unit potentials displayed the greatest peak-to-peak amplitude.¹⁴ The surface measurements of the motor unit potentials were made with the same multielectrode as for H-potential recordings (see above). The longitudinal poles of the multielectrode (poles 1–7) were aligned along the linea maxima with the transverse poles (poles 8–13, 14–19) aligned perpendicular to the linea maxima (Fig. 1D). The poles oriented perpendicular to the linea maxima recorded motor unit potentials in which the amplitude declined monotonically.

The motor unit recordings and the H-poten-

tials were amplified (bandwidth of 10 Hz to 10 kHz), displayed on a storage oscilloscope and recorded onto FM tape (bandwidth DC to 10 kHz). Peak-to-peak amplitudes of the motor unit and H-potentials were measured from the oscilloscope screen.

Isometric Force Recordings. The force of the isometric twitch contraction was recorded with a load cell strapped to the ankle joint and oriented perpendicular to the limb (Fig. 1B). The output from the load cell was directed to a transducer coupler and then displayed (oscilloscope) and recorded (FM tape) in the same way as the electromyographic recordings.

Experimental Protocol. Subjects were tested in a supine, semireclined position (Fig. 1B). The leg under investigation was held securely with hip and ankle straps that maintained the hip at 160°, and the ankle joint at a 110°. The knee angle could be changed from 100–150°, with 180° equal to complete extension. Subjects participated in one or more of the following tests.

1. Documentation of the shape and amplitude of the monopolar and bipolar H-potentials over the quadriceps femoris muscle was performed on 6 subjects. The leg muscles were relaxed and the knee joint was fixed at 100°. The H-potentials were elicited with constant submaximal stimulation. The longitudinal poles of the multielectrode (poles 1–7) were placed consecutively along the midline of rectus femoris, vastus medialis, and vastus lateralis, as well as along the borders between the vasti and rectus femoris (Fig. 2). The measurements were made along both the longitudinal and transverse poles. The measurements began 4 cm proximal to the patella and continued proximally until the amplitude of the H-potentials began to decline. The recordings were obtained by shifting the multielectrode. Each new site of the multielectrode placed the distal pole (pole 7) on the position of the former proximal pole (pole 1).
2. Three tests were performed on two subjects to determine whether the bipolar H-potential had one or two components (early and late). Because each of the following tests influence only the amplitude of the H-potential, the amplitude of the early component would remain constant if it was the M-wave

but would change if it was part of the H-potential. The first test applied a paired electrical stimulus to the femoral nerve with an intensity of about $1.5 \times$ H-reflex threshold and an interstimulus interval of 60 ms. The first stimulus conditions the pathway, thus significantly reducing the amplitude of the H-potential to the second (test) stimulus.²⁶ The second test utilized a voluntary contraction of the ipsilateral quadriceps muscle (<10% of maximum) that was maintained for 3 min while H-reflexes were evoked. Low levels of background muscle activity, similar to those used in this study, have been shown to increase the amplitude of the H-potential.³⁴ The third test utilized submaximal, isometric, Jendrassik maneuvers with three remote muscles: contralateral elbow flexors, jaw closure muscles, contralateral quadriceps femoris muscle. Jendrassik maneuvers have been shown to cause an increase in the amplitude of monosynaptic reflexes.^{6,33} Subjects contracted each muscle 10 times for 1–2 s with a 10-s rest between contractions. An H-reflex was evoked during each contraction and subsequently averaged.

3. Monopolar H-potentials from four subjects were investigated at different lengths of the quadriceps femoris muscle. The knee joint was fixed consecutively at 120°, 135°, and 150°. The limb was passively moved to each position by one of the investigators, beginning from a lengthened position and systematically shortening the muscle. The test started 1–2 min after the desired knee joint angle was reached and the subject was relaxed completely. Eight H-potentials were recorded at each knee joint position and subsequently averaged. The test was repeated several times until reproducible data were obtained. In addition, the shape and amplitude of 7 motor units were investigated. Two motor units were from vastus lateralis, 3 motor units were from rectus femoris, and 2 motor units were from vastus medialis. The subject maintained the voluntary activation of a single motor unit even during the transitions between the desired knee joint angles to ensure that action potentials from the same motor unit were being used as the reference for the spike-triggered average derived from the surface multielectrode.

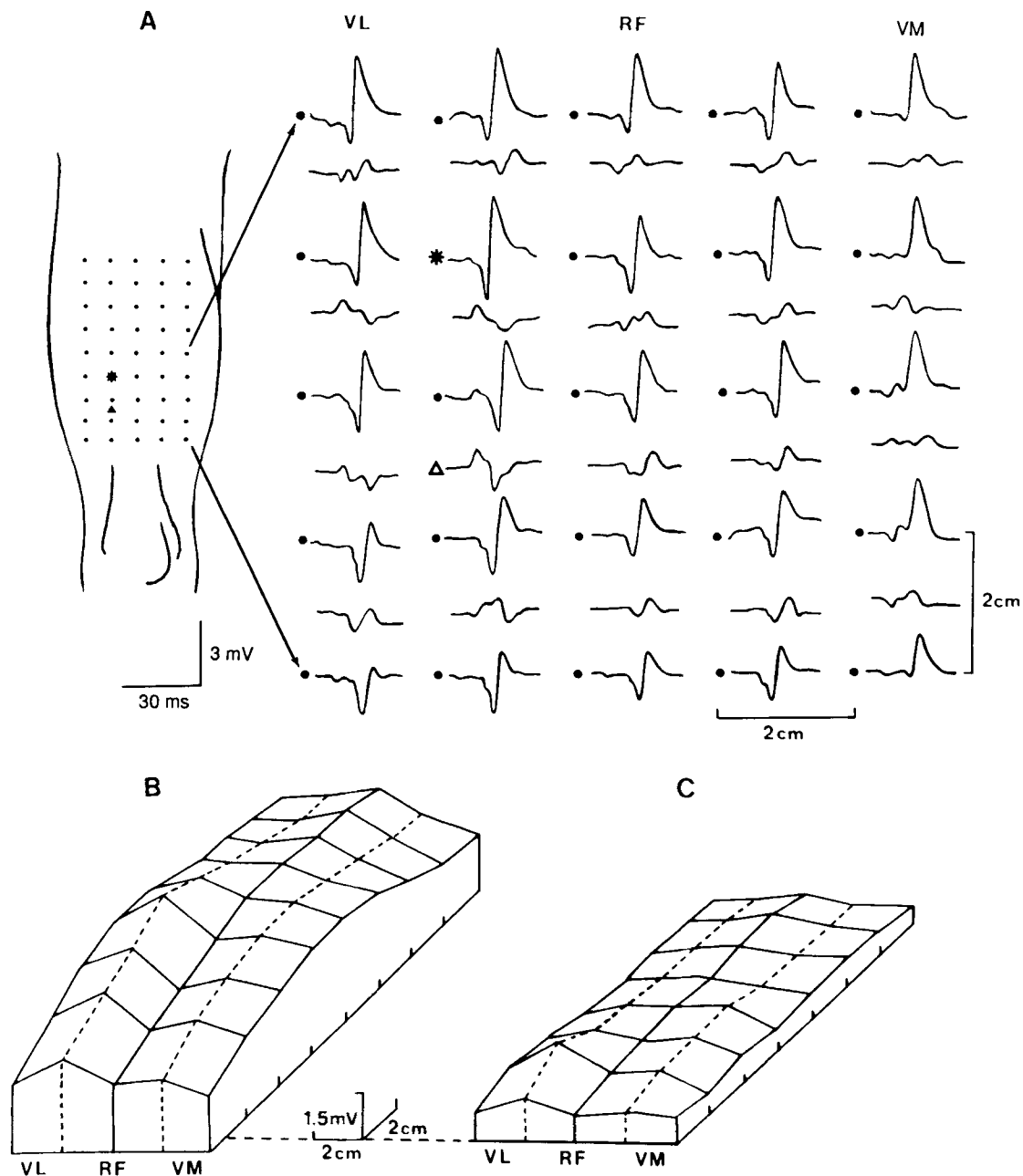


FIGURE 2. Documentation of the H-potentials over quadriceps femoris muscle. **(A)** The location of the multi-electrode (left) and the H-potentials recorded from each pole (right). The H-potentials in the right-hand panel correspond to the lower five rows (filled circles) of the multi-electrode position. The H-potentials include a monopolar measurement at each pole (filled circles over the thigh and beside the potentials) and a bipolar measurement between adjacent longitudinal poles; that is, the bipolar measurements appear between the biphasic monopolar measurements in each column. The asterisk indicates the location for the maximal monopolar H-potential recording, whereas the open triangle indicates the location for the maximal bipolar H-potentials. **(B, C)** The same data as in (A) are presented in a topographical projection for the monopolar H-potentials (B) and the bipolar H-potentials (C). The multi-electrode was positioned sequentially over the midline of vastus lateralis, rectus femoris, and vastus medialis (solid lines) and then over the border between vastus lateralis–rectus femoris and rectus femoris–vastus medialis (dotted lines).

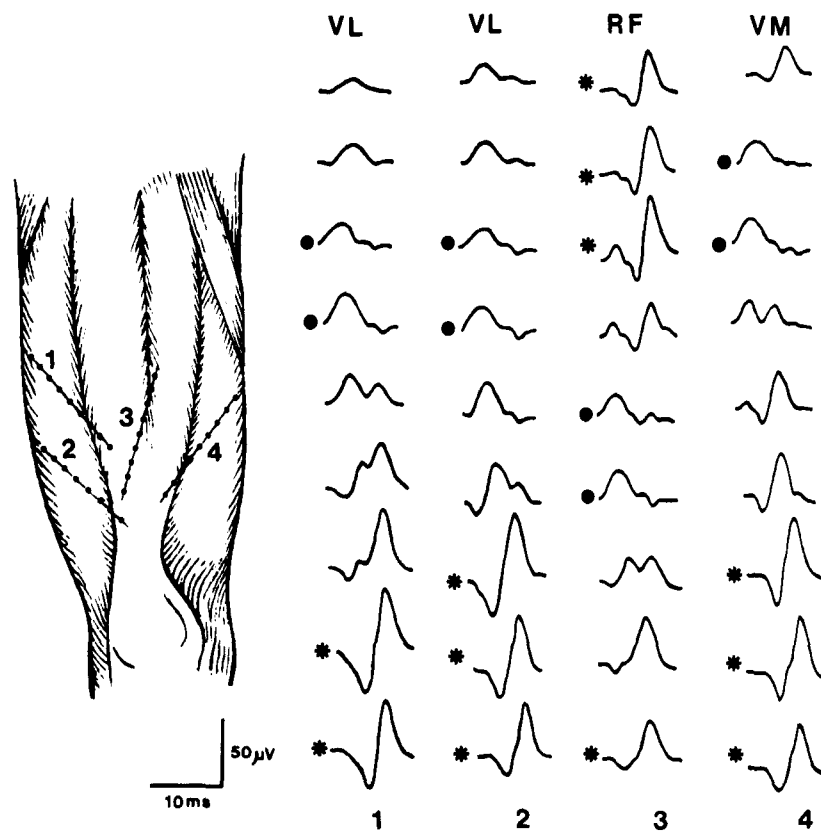


FIGURE 3. Determination of the linea maxima. Monopolar potentials for four motor units measured along the skin surface (1 and 2 from vastus lateralis, 3 from rectus femoris, 4 from vastus medialis). The linea maxima of the motor units are marked with the solid lines on the left. The 9 motor unit potentials along each linea maxima are on the right; each trace is an average of 128 potentials. The motor unit potentials with biphasic shape and large peak-to-peak amplitude are indicated with an asterisk, while the motor unit potentials comprising an initial negative phase followed by one or two positive phases are denoted with filled circles.

RESULTS

Location for Recording Maximal Quadriceps Femoris H- and Motor Unit Potentials. With the muscle relaxed and at a fixed length (knee joint set at 100°), the monopolar and bipolar recordings gave reproducible H-potentials. The latency from the stimulus to the onset of the monopolar H-potentials was between 16 and 19 ms. At times, the exact measurement of the onset of the H-potential was impeded by the preceding M-response. The duration of the H-potentials ranged from 25 to 28 ms.

In 5 of the 6 subjects, the amplitude of the monopolar H-potentials was maximal between 9 and 17 cm proximal to the patella and 1.5–2 cm lateral to the midline of rectus femoris, approximately over the border between vastus lateralis and rectus femoris. In the sixth subject, the location for the maximum amplitude monopolar H-potential was 12 cm proximal to the patella but 3.5 cm lateral to the midline of rectus femoris; thus, for this subject, the amplitude of the H-potentials was maximal over vastus lateralis. When the location for the

maximal monopolar H-potentials was expressed as a percent of thigh length (greater trochanter to patella), the location fell between 24% and 35% of thigh length as measured from the patella, with a mean of $29 \pm 4.2\%$ (mean \pm SD). The corresponding optimal location for bipolar H-potentials was distal to that for monopolar H-potentials by 1–3 cm. The optimal locations for the monopolar and bipolar H-potentials of 1 subject are depicted in Figure 2. The changes in amplitude of the H-potential over the area of quadriceps femoris are clearly evident.

As with the H-potentials, the location for recording the maximum-amplitude surface motor unit potentials (linea maxima, see Methods) was determined. The direction of the linea maxima coincided with the direction of the muscle fibers. The linea maxima of motor units in rectus femoris diverged from its midline obliquely downward (to each side), in vastus medialis the linea maxima was directed obliquely downward and laterally, in vastus lateralis the linea maxima ran downward and

medially (Fig. 3). Even along the linea maxima, the motor unit potentials displayed significant changes in shape and amplitude. For motor units in vastus lateralis and medialis, the largest peak-to-peak amplitude of the motor unit potentials were distal over the boundaries between the vasti and the rectus femoris muscles. For motor units in rectus femoris, the peak-to-peak amplitudes were largest proximally over the midline of rectus femoris.

Monopolar and Bipolar Measurements of Quadriceps Femoris H-Potentials. The shape of the monopolar H-potentials over vastus lateralis and rectus femoris muscles was consistently biphasic, comprising an initial positive and a terminal negative phase (Fig. 2A). In contrast, the shape of the bipolar H-potentials varied from biphasic to polyphasic but not in any consistent manner (Fig. 2A). Although the monopolar H-potentials showed

modest variations in shape, the waveform of the associated bipolar H-potentials was quite unpredictable. The peak-to-peak amplitudes of the monopolar H-potentials were substantially higher than those bipolar recordings from the same area of the skin. The amplitude of both the monopolar and bipolar H-potentials varied along the mapped area over quadriceps femoris muscle but were found to have maximal amplitude over the lateral aspect of the muscle (Fig. 2B, C).

The polyphasic shape of the bipolar H-potential gave the impression that the H-potential had more than one component, although corresponding components were not evident in the monopolar H-potentials (see Fig. 4, subject 2 on the left). Because the existence of two (early and late) components in quadriceps femoris H-reflex was based on bipolar H-potentials,²⁵ we measured simultaneously both monopolar and bipolar H-potentials. The polyphasic nature of the bipolar H-potential

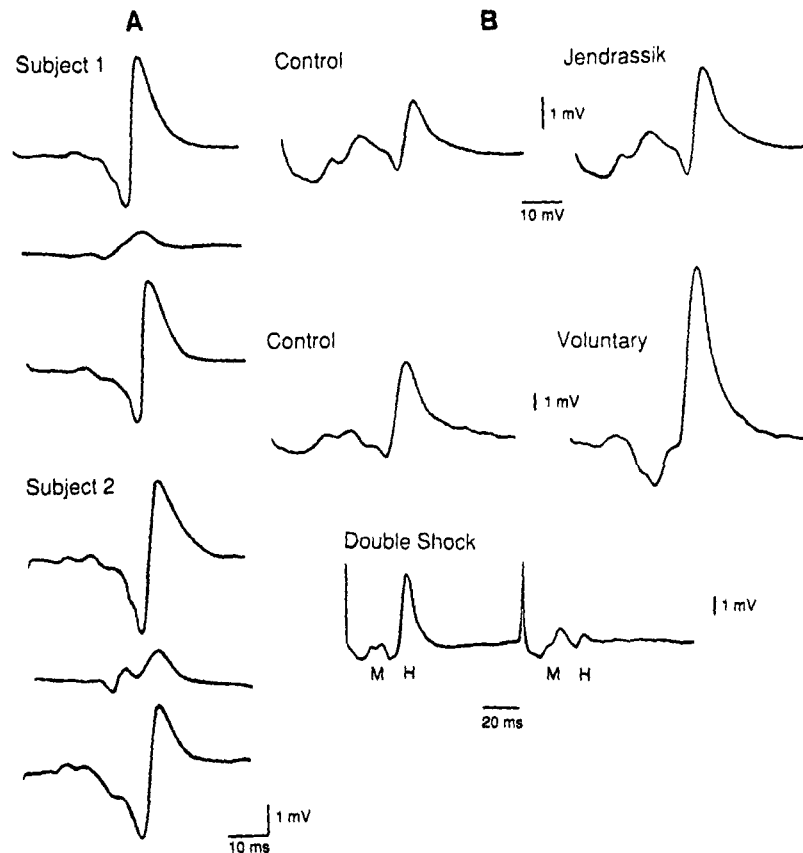


FIGURE 4. Discrimination of H-potential components. **(A)** Averaged monopolar and bipolar H-potentials in 2 different subjects. The upper and lower traces for each subject represent monopolar H-potentials and the middle trace represents the bipolar H-potential. Each trace is an average of 8 trials. **(B)** The three tests used to distinguish the components of the H-potential. The top two traces correspond to the control monopolar H-potential (left) and the H-potential during the Jendrassik maneuver (right) with contraction of the elbow flexors. The middle two traces show the control monopolar H-potential (left) and the H-potential during moderate voluntary contraction of the ipsilateral quadriceps femoris muscle. The lower trace shows the effect of paired electrical stimulation on the two components. All three procedures do not affect the initial component (M response) but influence only the amplitude of the later biphasic complex (H-potential).

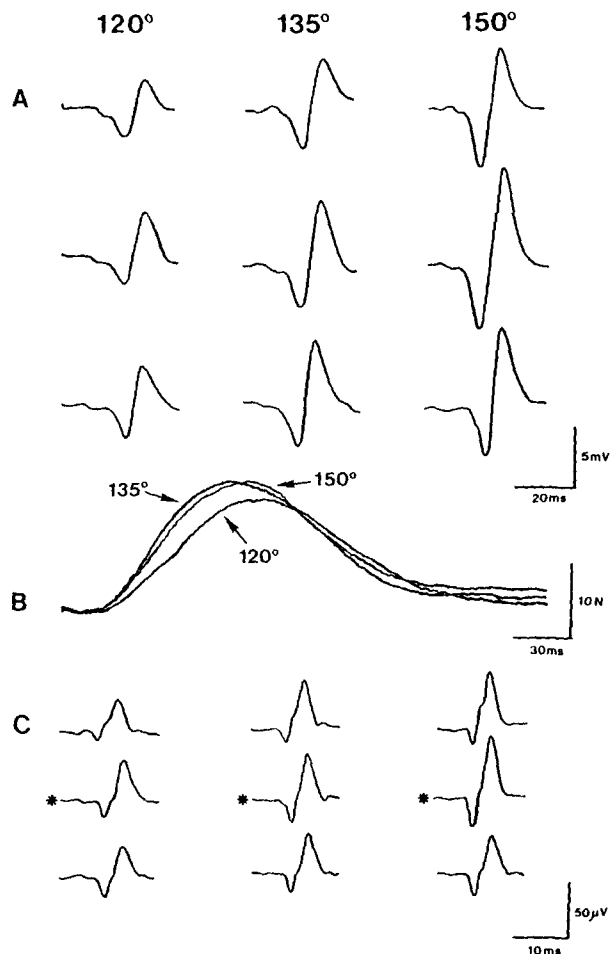


FIGURE 5. Effects of a change in the length of passive muscle on the H- and motor unit potentials. **(A)** Three sets of monopolar H-potentials simultaneously measured from the location that produced the maximal-amplitude potentials (middle trace), 1.0 cm proximally (upper trace) and 1.0 cm distally (lower trace). Each trace is an average of eight trials. The knee joint was consecutively set at 120°, 135°, and 150° which meant that quadriceps femoris changed from a long to a short length. **(B)** Twitch force measured at the ankle for each of the knee joint angles. **(C)** Averaged monopolar motor unit potentials ($N = 128$) recorded along the linea maxima. The asterisks indicate the potentials with the greatest peak-to-peak amplitude at each knee joint angle.

could have resulted from either: (1) differences in the timing and amplitude of the monopolar H-potentials; or (2) inclusion of the M-wave in the H-potential. To distinguish between these possibilities, three tests were performed that are known to influence the amplitude of H-reflex responses: the Jendrassik maneuver, submaximal voluntary contraction, and conditioning stimuli. The Jendrassik maneuvers and submaximal voluntary contractions of the ipsilateral quadriceps muscle facilitated only the later biphasic "component" of the H-po-

tential (Fig. 4). Furthermore, when two electrical stimuli (conditioning and test) were delivered in short succession (60 ms), the later "component" was markedly reduced while the earlier wave was relatively unaffected (Fig. 4). These findings suggest that the earlier component is, in reality, the M-response and only the later component is the H-potential.

Effects of Passive Muscle Length Changes. Passive stepwise shortening of the relaxed quadriceps femoris muscle, from 120° to 150°, resulted in a marked increase in the amplitude of the monopolar H-potential. This is evident in the data from one subject in Figure 5. Three monopolar H-potentials (Fig. 5A) were measured simultaneously from the location that produced the maximum-amplitude potentials (middle trace), 1.0 cm proximally (upper trace) and 1.0 cm distally (lower trace). The amplitude of the H-potentials increased by 95–170% (mean \pm SD: 136 ± 35) in all 4 subjects when the knee angle was changed from 120° to 150° and the muscle was shortened. The maximal amplitude of the motor unit potentials, measured along the linea maxima (asterisk in Fig. 5C), increased by 30–75% (53 ± 16). Thus, the percentage increase in the amplitude of the motor unit potentials was lower than that obtained for the H-potentials. As would be expected from the length-tension relationship, the twitch force (Fig. 5B) was largest at the intermediate angles (135–150°).

DISCUSSION

Muscle architecture is known to influence the shape and amplitude of the motor unit and the H-potentials recorded on the skin surface.^{8–10, 15, 16, 23} The quadriceps femoris muscle has a complex architecture. The rectus femoris is a bipennate muscle with fibers originating proximally in a long thin central tendon and diverging obliquely downward (to each side) to insert in a wide aponeurosis leading to the patellar tendon (Fig. 3). The fibers of the vastus medialis run obliquely downward and laterally, whereas the fibers of the vastus lateralis are directed obliquely downward and medially. The muscle fibers³⁵ are relatively short (mean length of 60–70 mm) and the angle of pennation varies between 0–5° with the exception of the distal portions of both vasti that have pennation angles of 30–45°. The endplate zone is broad with orientation in different planes.^{4,7,19,20,30}

An idealized diagram of the distal parts (IDP) of the quadriceps femoris muscle is presented in

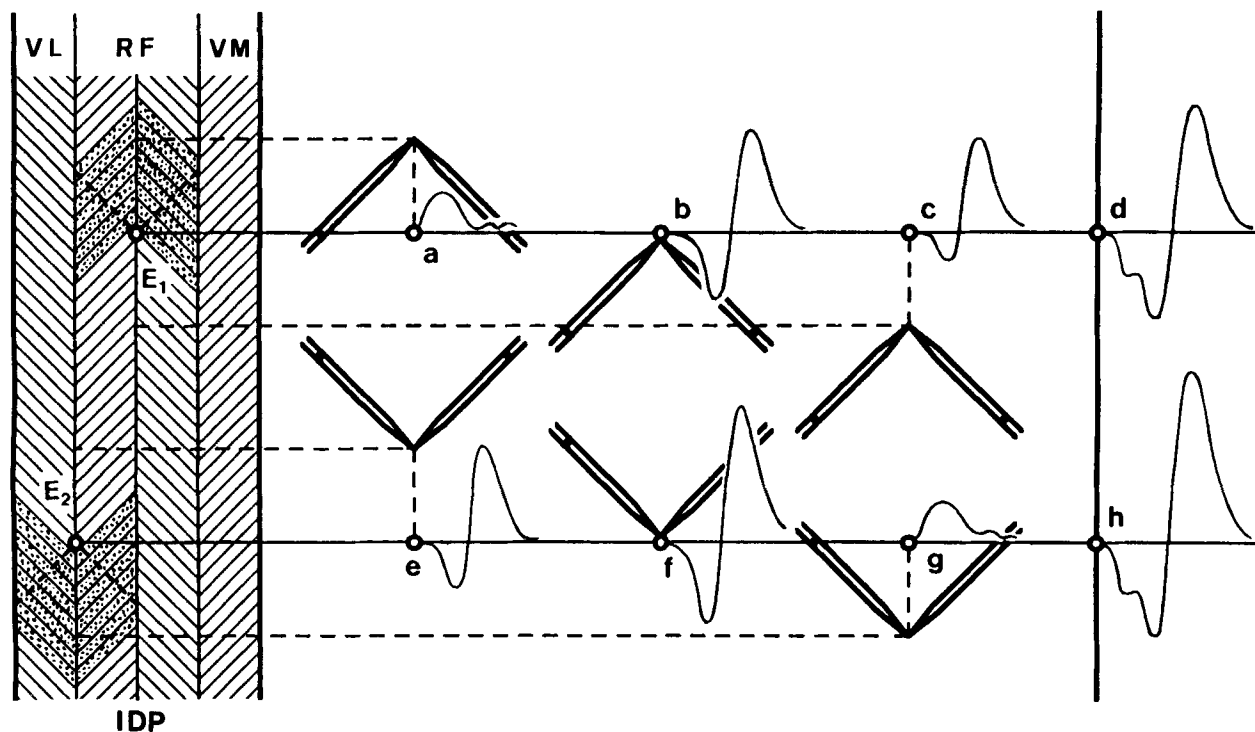


FIGURE 6. Interaction between muscle architecture and muscle fiber potentials. The scheme shows an idealized muscle architecture for the distal part (IDP) of quadriceps femoris (left panel), the relationship between electrode location and the shape and amplitude of muscle fiber potentials (middle panel; a-c, e-g), and net H-reflex potentials (right panel; d and h). The middle panel shows the effect of electrode location relative to pairs of active muscle fibers. The upper row (middle panel) shows three combinations for rectus femoris while the lower row shows three combinations for the boundary between rectus femoris and vastus lateralis. In each case, the open circle indicates the location of the electrode. The horizontal dashed line from the pointed end of each pair of muscle fibers to the muscle (left panel) indicates the critical location of the electrode relative to the active muscle fibers (stippled). When the dashed line intersects (a, g) the stippled area (active muscle fibers), the electrode is considered to be "over" the fibers. In contrast, when the dashed line does not intersect the stippled area, the electrode is at the end (b, f) or beyond the end (c, e) of the active muscle fibers. See text for further explanation of these interactions.

Figure 6. The muscle fibers are arranged in four vertical columns, with vastus lateralis and vastus medialis represented as unipennate muscles and rectus femoris shown as a bipennate muscle. The insertions of the muscle fibers from both vastus lateralis and vastus medialis converge with fibers from rectus femoris in a downward, oblique design. The origins of the lateral and medial aspect of rectus femoris converge in an upward, oblique arrangement.

Location for Recording Maximal-Amplitude Quadriceps Femoris H-Potentials. The shape and amplitude of the motor unit and H-reflex potentials correspond to the architecture of the quadriceps femoris muscle and the peculiarities of the extracellular potential field in striated muscle. They were similar to motor unit and H-reflex potentials for muscles with short fibers (e.g., triceps surae), as described previously.^{9,10,15-18} The H-reflex and motor unit action potentials measured over a large

region of quadriceps femoris muscle are generated mainly by the underlying parts of vastus lateralis, rectus femoris, and vastus medialis located close to the skin. The greatest peak-to-peak amplitudes for the motor unit potentials occurred at the distal ends of vastus lateralis and vastus medialis fibers and the proximal ends of rectus femoris fibers (Fig. 4, motor unit potentials with asterisks).

The shape of the potentials can be explained by the idealized architecture shown in Figure 6. Consider two monopolar electrodes placed on the skin over the muscle, one at the midline of the rectus femoris (E_1) and the other at the border between vastus lateralis and rectus femoris (E_2). The middle section of Figure 6 shows the extracellular action potentials recorded by the electrodes for six pairs of active muscle fibers (stippled area). When the electrode is located *over* the pair of fibers (Fig. 6 a, g), the action potential begins with an initial negative followed by one or two positive phases. The electrode is described as "over" the pair of fibers

when the horizontal line drawn from the point of recording (E_1 and E_2) passes through the fiber (Fig. 6 a, g). In contrast, when the electrode is located *at* (Fig. 6 b, f) or *beyond* (Fig. 6 c, e) the end of the pair of muscle fibers, the potentials are biphasic and comprise an initial positive and subsequent terminal negative phase. The electrode is "beyond" the muscle fiber when the horizontal line drawn from the point of recording (E_1 and E_2) to the muscle fiber passes through its end or an imaginary continuation (Fig. 6 c, e). The peak-to-peak amplitude of the biphasic potentials was greatest when the electrode was at the ends of the active fibers (Fig. 6 b, f) and the amplitude decreased monotonically with increasing distance from the fibers (Fig. 6 c, e).

Consequently, the motor unit potentials measured along the linea maxima displayed shapes that were typical for electrode locations "over" the fibers (Fig. 3, filled circles), "beyond" the fibers (Fig. 3, asterisks), and various combinations of the two. Thus, the motor unit potentials measured at or beyond the ends of the muscle fibers had the largest peak-to-peak amplitudes (Fig. 3, potentials marked with asterisks), compared to the motor unit potentials recorded above the muscle fibers (Fig. 3, potential marked with filled circles). Accordingly, we found that the greatest peak-to-peak amplitudes for the motor unit potentials occurred at the distal ends of vastus lateralis and vastus medialis fibers, and the proximal ends of the rectus femoris fibers.

Because the relatively short muscle fibers of quadriceps femoris are oriented in different directions, a recording electrode located on the skin surface will always be over some active muscle fibers and beyond the ends of other active fibers. The net H-reflex potentials are dominated by the large potentials that can be recorded at and beyond the ends of the fibers and are volume conducted over long distances to the recording electrode.¹⁰ Consequently, the characteristic shape of motor unit potentials is biphasic (Fig. 6 d, h). However, the initial phase of the biphasic potentials can be modified (see hump in Fig. 6 d, h) by potentials recorded from active fibers located beneath the electrode (Fig. 6 a, g), as has been observed for triceps surae H-potentials.^{9,10} The location for recording maximal monopolar H-potentials (Fig. 2A) in the majority of subjects was along the border between the rectus femoris and vastus lateralis (E_2 in Fig. 6). In this region of the muscle, the number of motor units for which the electrode is beyond the muscle

fiber ends increases. The location of the maximal H-potential corresponds to the site at which the summation of these motor unit potentials is maximal.

The location for recording the maximal bipolar H-potentials lies distal to that for monopolar H-potentials. In this region, the timing and amplitude of the monopolar H-potentials recorded at adjacent poles demonstrate the largest differences because of changes in length, inclination, and pennation of the muscle fibers.

Monopolar and Bipolar Measurement of Quadriceps Femoris H-Potentials.

The complex architecture of the quadriceps femoris muscle results in a great variety of shapes and amplitudes of the H-potentials, particularly for the bipolar H-potentials. Because the monopolar H-potentials were more consistent in shape and amplitude than bipolar H-potentials, monopolar recordings permit an easier distinction of the M-response and the H-potential. In contrast to an earlier suggestion based on bipolar H-potentials,²⁵ we found no evidence in the monopolar records that the H-potential consisted of two components (early and late). The Jendrassik maneuver, submaximal voluntary contraction, and conditioning stimuli influenced only the amplitude of the biphasic (late) component, which is evidently of reflex origin. An early component in the bipolar H-potential is a result of differences in timing and amplitude of the associated monopolar H-potentials or the M-response contamination of the H-potentials. Because the reflex pathway in the quadriceps femoris muscle is short compared to the triceps surae muscle, the M-response can overlap with the H-potential and hence modify the shape of the H-potential.

Effect of Passive Muscle Length Changes. The observation that passive shortening of quadriceps femoris muscle causes an increase in the amplitude of the monopolar H-potentials confirms previous data of Guiheneuc and Ginot,¹² which were obtained with bipolar measurements. Similar data have been reported for soleus bipolar H-potentials^{3,21,24,27} and monopolar H-potentials.^{8,10} These amplitude changes cannot be explained by changes in monosynaptic reflex excitability alone. In quadriceps femoris muscle, it appears that both central and peripheral factors are implicated.

1. *Central factors:* The amplitude of the H-reflex depends on the excitability of the motor

neuron soma and the level of presynaptic inhibition of the Ia terminal.³² Reduction of transmitter release at Ia terminals for several seconds has been suggested to be responsible for the depression of H-potentials during ramp increases in muscle length.^{2,5} In the present experiments, however, we started from a lengthened position and systematically shortened the muscle. It is conceivable that shortening the muscle reversed any postactivation depression induced by the passive stretch, thus allowing the H-potentials to enlarge. Previous authors have associated the reduction in H-potential amplitude due to muscle stretching with reflex inhibition of the alpha motor neuron pool caused by muscle spindle or Golgi tendon organs.^{13,31} These studies, however, were performed on soleus muscle and the peripheral contribution to changes in H-potential amplitude was sizable.¹⁰ In quadriceps femoris, while the motor unit potentials increased with muscle shortening, the magnitude of the increase was insufficient to account for the larger increase in the H-potential.

2. *Peripheral factors:* Shortening the muscle can cause an increased inclination of the muscle fibers relative to the skin surface, which shortens the depolarized area and increases the amplitude of the H-potentials. These changes have been well documented in soleus muscle (see Fig. 10 in ref. 10). According to Morimoto,³⁰ the length of human vastus medialis fibers is about 65 mm at a knee joint angle of 90°, and about 36 mm at complete extension (180°). These changes in fiber length would increase the muscle fiber diameter and cause an increase in the amplitude of the H-potentials.

Because of the uncertainty surrounding the relative contribution of peripheral and central factors underlying changes in H-potential amplitude, it is important to compare simultaneously the single motor unit amplitude with that of the H-potential. The data indicate that some of the length-related changes in the amplitude of the H-potential are due to changes in the architecture of the quadriceps femoris muscle. Consequently, H-potential amplitude does not provide a direct index of monosynaptic reflex excitability. Furthermore, these peripheral factors can cause changes in the

amplitude of whole-muscle EMG that are independent of changes in the neural drive to muscle.

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