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Single Fibre Action Potentials in Skeletal Muscle Related to Recording Distances

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Summary: Single muscle fibre action potentials (SFAPs) are considered to be functions of a bioelectrical source and electrical conductivity parameters of the medium. In most model studies SFAPs are computed as a convolution of the bioelectrical source with a transfer function. Calculated peak-to-peak amplitudes of SFAPs decrease with increasing recording distances. In this paper an experimental validation of model results is presented. Experiments were carried out on the m. extensor digitorum longus (EDL) of the rat. Using a method including fluorescent labelling of the active fibre, the distance between the active fibre and the recording electrode was derived. With another method, the decline of the peak-to-peak amplitude of SFAPs detected along a multi-electrode was obtained. With both experimental methods, in general peak-to-peak amplitudes of SFAPs decreased with increasing recording distances, as was found in model results with present volume conduction theory. However, this behaviour was not found in all experiments. The rate of decline of the peak-to-peak amplitudes with recording distance was always less than in models.

Key Words: Single fibre electromyography—Wire electrodes—Multi-electrode—Rat muscle—Fibre labelling.

INTRODUCTION

Electrical signals generated by skeletal muscles provide maximal information about their origins if measured by electrodes within or in close proximity to the active fibres. It is well known that due to the volume conductor the shape of an extracellular action potential depends on the position of its recording site with respect to the active fibre[3,17,18]. In needle multi-electrode recordings[8–10] the single fibre action potential (SFAP) with the highest peak-to-peak amplitude was assumed to be measured very close to the active fibre. A smoothly declining function was considered to fit the amplitudes of the SFAPs along the needle[8,9]. New possibilities for studying the effect of the volume conductor were gained with the scanning EMG technique[10]. The scanning EMG results were interpreted in an identical way to the needle multi-electrode results.

A disadvantage in the cited human muscle rec-

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ordings is the fact that the absolute distance between the active fibre and the recording site could not be measured. In order to obtain a relation between SFAP parameters and recording distance, an experimental method for the recording of SFAPs at known distances from the active fibre was introduced in animal muscle[4,22]. The active fibre was labelled by injection of a fluorescent dye and positions of recording wire electrodes were marked by deposition of small silver layers. However, these experiments yielded insufficient data to allow for general conclusions to be reached. Sometimes peak-to-peak amplitudes of SFAPs even increased with increasing recording distance.

In model studies, SFAP parameters could easily be related to recording distances. SFAPs were computed as a convolution of a chosen source function with a transfer function, calculated from volume conduction parameters and taking into account the recording distance. Without exception peak-to-peak amplitudes of SFAPs decreased with increasing recording distance. This finding was independent of the characteristics of the bio-electrical source[9,13,20]. Properties of the volume conductor were frequently a subject of study. In many studies homogeneous volume conduction parameters were assumed[6,7,11,12]. Others took into account the frequency dependent, fibrous structure of muscle tissue[2,14,15,17,18]. The effect of the presence of inhomogeneities, such as connective tissue and blood vessels were also studied[18,19]. When comparing model results[17–19] to experimental data[4,22] the resemblance at equal recording distances was found to be insufficient.

The objective of the present paper is to augment experimental data regarding the relation between SFAP parameters and recording distances. Two experimental procedures were used. The first one was basically the same as used before[4]. In this procedure, SFAPs were measured with wire electrodes. The active fibre as well as the recording sites were labelled, yielding the absolute recording distances. In the second procedure, a thin needle with eight electrodes (multi-electrode) was used, in the same experimental conditions. Here the absolute distance between different recording electrodes was known, rather than the distance between the active fibre and the recording site. Such needle recordings were easier to obtain and enabled comparison with literature. The results of both procedures were compared and evaluated in the context of results from simulations performed with detailed models.

METHODS

Muscle Preparations

Experiments were carried out *in vivo* on the m. EDL of the rat (Wistar, generally 3–5 months old, weighing about 0.3 kg). For each experiment a separate rat was used. In wire electrode experiments 55 rats were used and 25 in experiments with a multi-electrode. The animals were anaesthetized with Nembutal. Muscle temperature was about 308 ± 1 K. A detailed description of the preparation of the EDL and anaesthesia during the experiments was given elsewhere[21]. The procedures were approved by the animal experiment ethical committee of the University of Twente.

Stimulating Electrodes

Activity of one single fibre was evoked with a micropipette. Tip diameters were between 1–2 μm; impedances were between 5–10 MΩ when placed on the muscle surface. The electrodes were filled with a 0.5 M LiCl solution. The micropipette was moved into the muscle with fast steps of 5 μm. The distance between the pipette and the nearest recording electrode was at least 4 mm. A decrease of at least 60 mV at the tip of the micropipette indicated penetration of a muscle fibre. Fibres were stimulated by a hyperpolarizing rectangular current pulse with a duration of 40 ms and an amplitude between 250–400 nA. Stimulation resulted in one or more intracellular action potentials, recorded at the tip of the micropipette.This form of experimentation was nearly the same as the procedure described by Albers et al.[4].

Procedure 1: Locating the Active Fibre and Recording Sites; Wire Electrode Recordings

In this procedure, SFAPs were recorded with a 14 channel array wire electrode arrangement[4,22]. The Ni-Cr core had a diameter of 25 μm. Wires were insulated with a 4 μm thick Karma coating. They were cut at an angle of about 45°. Tips were coated with a small silver layer. The wires were inserted into the m. EDL one by one, in rows of two or three electrodes, at an angle of about 45° to the muscle surface. Impedances of the wire electrodes were between 10–30 kΩ (frequency between 500 Hz and 10 kHz). Properties of wire electrodes and cabling to the amplifier (input

impedance $10^{14}\Omega$ // 3pF) caused low-pass filtering effects. When the signal comprised high frequencies, it was found experimentally that the peak-to-peak amplitudes could be reduced maximally by 20%. The electrical behaviour of identically treated electrodes per experiment was comparable. A large reference electrode was positioned at the m. tibialis anterior.

The micropipette was inserted in the muscle at those places where muscle fibres were found extending to the area with recording electrodes. The direction of the muscle fibres was observed by a microscope. Activity of one single fibre was evoked as described above. When no acceptable extracellular signals (with peak-to-peak amplitudes well above the noise level) were measured, the pipette was retracted and moved 200 μm in the medial, lateral or rostral direction. In general, 5–10 different positions of the micropipette were tried before acceptable SFAPs were recorded. SFAPs were low-pass filtered (cut off frequency 20 kHz, 12 dB octave^{-1}). They were digitally stored after sampling at a rate of 100 kHz and AD conversion (10 bit resolution, 4096 samples per channel).

For labelling the active fibre, a fluorescent dye Lucifer Yellow CH (the di-lithium salt, Sigma) was used[4]. Dye concentration was 50 mg ml^{-1}, and it was dissolved in the 0.5 M LiCl solution in the micropipette. When at least one acceptable extracellular response on the wire electrodes was recorded, the stimulated fibre was labelled by iontophoresis of Lucifer Yellow CH out of the micropipette. Iontophoresis was carried out by hyperpolarizing current pulses with an amplitude of 40 nA, 1 s on and 1 s off. To achieve reliable fibre labelling, it was necessary to apply at least 600 pulses. During iontophoresis, pipette impedance and resting membrane potential were monitored. A sudden increase in the resting membrane potential indicated that the pipette no longer resided in the fibre. A significant increase in the pipette impedance indicated electrode blocking. In both cases iontophoresis was stopped. After labelling, the micropipette was retracted.

Silver layers were electrophoretically deposited from the tips of those wires that had recorded acceptable SFAPs. To achieve this, a DC current of 1 μA was applied for 30 s. All wires were carefully removed afterwards[4]. In the method described by Albers et al. electrodes that had recorded acceptable SFAPs were cut above the muscle surface; the other electrodes were removed. A major drawback of that method was the fact that slices were frequently of poor quality due to damage by the knife upon cross-sectioning the wire. This prevented reliable observation of the muscle structure. Silver deposits marked the recording positions of the wire electrodes. The muscle was removed from the animal, quickly frozen avoiding change in length, and stored at a temperature of about 193 K. The time passing between termination of the iontophoresis and freezing of the muscle was about 15 min.

The muscle was sectioned into slices (10 μm thick) on a cryostat at a temperature of 248 K. Autofluorescence (emission wave length 540 nm) of Lucifer Yellow CH was observed in a single muscle fibre, marking the stimulated one. Photographs were taken from cryosections with autofluorescence. Fluorescence in the active fibre showed up over a length ranging from 100 μm to 3 mm from the position of the micropipette. The nonfluorescent part of the stimulated active fibre was traced from slice to slice until a silver deposit from a wire electrode was found. This procedure was continued until the position of the active fibre was known for all slices with silver deposits. Silver deposits were traced in the native cryosections using a bright field reflection microscope. The silver deposits reflected light making them distinguishable from other dark disturbances in the slice. Recording distance could thus be obtained. It was defined from the centre of the active fibre to the centre of the silver deposit.

Procedure 2: Multi-electrode Measurements, Relative Recording Positions

In a rectanglar window at the side of a stainless steel injection cannula with a diameter of 0.3 mm, eight wire electrodes were arranged (Figure 1). Recording electrodes were the cut ends of Ni-Cr wires as described before. The wires were embedded in heat hardened epoxy resin and positioned in a row, with an in-between distance of 133 ± 5 μm. The recording electrodes were coated with a thin silver layer to lower the impedance. Impedances varied between 20–70 kΩ, depending on the frequency (between 500 Hz and 10 kHz). The tip of the needle was polished after every five or six experiments. The multi-electrode was inserted into the EDL muscle at an angle of about 45° with the muscle surface. Its position was generally near the midsection in the rostral part of the muscle. During each experiment, the needle remained at one position. The upper electrode was at least 1 mm

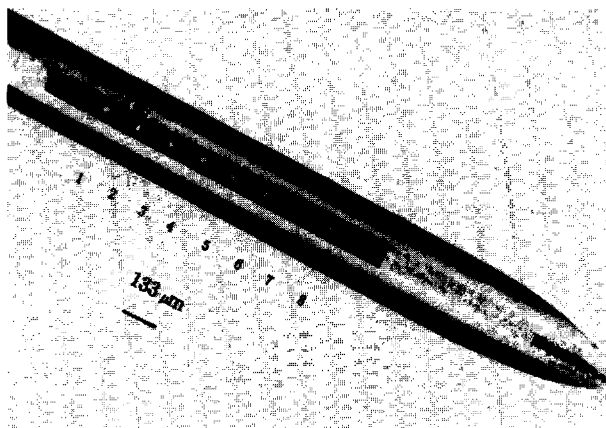


FIG. 1. The multi-electrode. The electrodes are numbered 1–8; the distance between the centres of two electrodes is 133 μm. Since only seven signals could be recorded and stored at the same time, electrode no. 8 was not used during the experiments.

beneath the muscle surface. Here again a large reference electrode was inserted in the m. tibialis anterior.

Activity of a single fibre was evoked with a micropipette as described before. Since it was not the aim of this experimental procedure to label the active fibre, the pipette was not filled with Lucifer Yellow, but with 0.5 M LiCl solution only. The longitudinal distance between the micropipette and the recording sites in the multi-electrode was at least 4 mm. The muscle was searched for fibres with the pipette, along a path from lateral to medial or vice versa. The first path was generally at a longitudinal distance of about 8–10 mm from the multi-electrode. Extracellular recordings were digitally stored, as described above. After completing one path, the pipette was moved 400 μm in the rostral direction and the procedure was repeated. The distance between two trials in one path was approximately 200 μm. Experiments were stopped when the longitudinal distance between the pipette and the multi-electrode was 4 mm.

After two experiments the muscle was removed from the animal in order to test possible muscle damage caused by the needle. Changes in length were carefully avoided. After quick freezing and sectioning into 10 μm slices, needle traces could not be found.

Noise levels in the muscle were tested by recording with the multi-electrode without stimulating a fibre. Root mean square (rms) values were comparable for all recording electrodes (about 10 μV).

Computed SFAPs

Measurements were compared to model results reported before[18]. SFAPs were computed as convolutions of a source function with a transfer function describing volume conduction parameters. The model was described earlier in detail[1–3,17–20]. It accounts for the fibrous, frequency-dependent structure of muscle tissue. Anisotropy is also incorporated. The muscle part of the model was given a radial bound (diameter 3 mm) and was cylinder-shaped. The muscle was suspended in air, thus reflecting the experimental conditions. Microscopic conductivity parameters were derived from the literature[2]. The source function was taken according to the model proposed by Rosenfalck[13].

RESULTS

SFAP Characteristics

SFAPs measured either by wire electrodes or by the multi-electrode were characterized by their peak-to-peak amplitude V_{tt}, the time interval Δt between the maxima of the first phase and the second phase and by V_1, the amplitude of the first phase. Figure 2 depicts an example of a measured SFAP recorded on a wire electrode. In Figure 3 an example of simultaneous SFAP recordings at electrodes 2–7 of the needle are shown. Characteristics of SFAPs recorded with both experimental procedures (described in the Methods section) were compared. Because procedure 2 did not yield absolute recording distances, Δt and V_1 were plotted as functions of V_{tt} (Figures 4 and 5, respectively). Differences between characteristics of SFAPs meas-

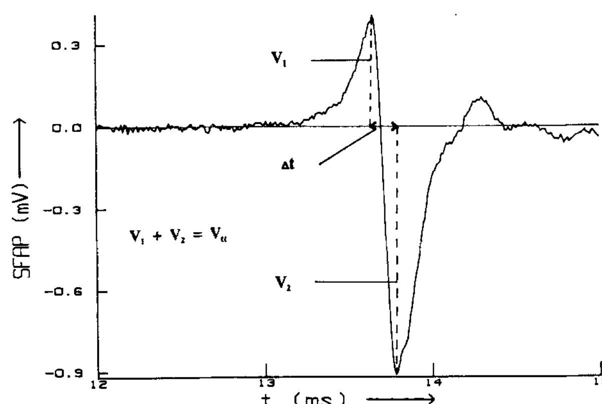


FIG. 2. An example of a SFAP, measured using a wire electrode. SFAP characteristics V_{tt}, V_1 and Δt are indicated.

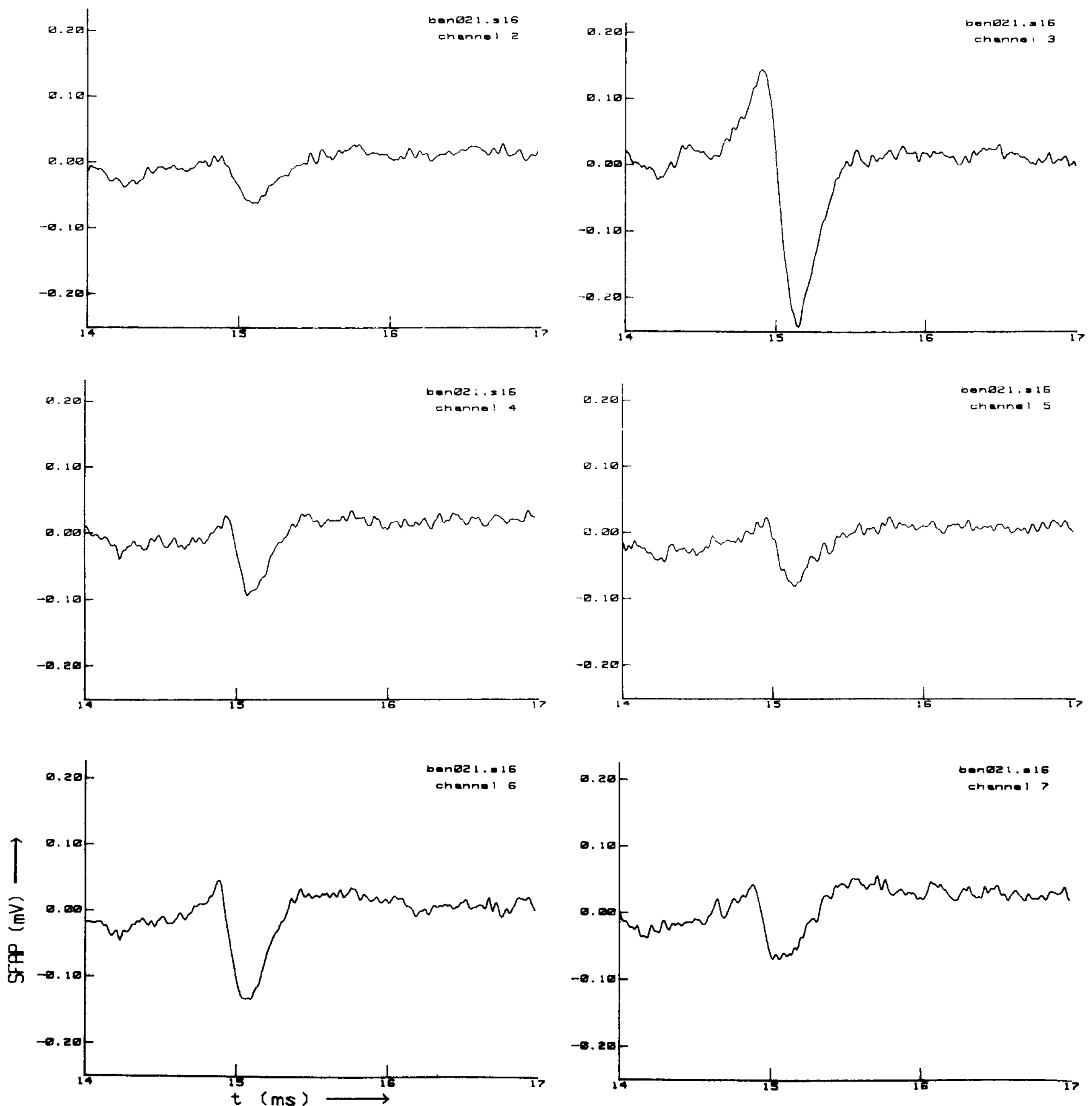


FIG. 3. Typical example of a registration with the multi-electrode (six channels plotted). Channel numbers refer to the electrode numbers in Figure 1. The maximum peak-to-peak amplitude in this registration was found on electrode 3. Note the local maximum on electrode 6. The decline of the peak-to-peak amplitude along the needle of this registration is depicted in Figure 8 (experiment ben021b, line marked with circle symbols).

ured with wire electrodes and those measured with the multi-electrode were not significant (Student test, $P< 0.01$). Characteristics of SFAPs obtained with both experimental procedures were therefore comparable. Parameter V_{tt} appeared to be least sensitive to disturbances caused by noise. Therefore, V_{tt} was used to study SFAPs with respect to the positions of their recording sites.

Procedure 1: Wire Electrode Results

Lucifer Yellow CH was found in the labelled fibre over a length of 100 μm to 3 mm. During

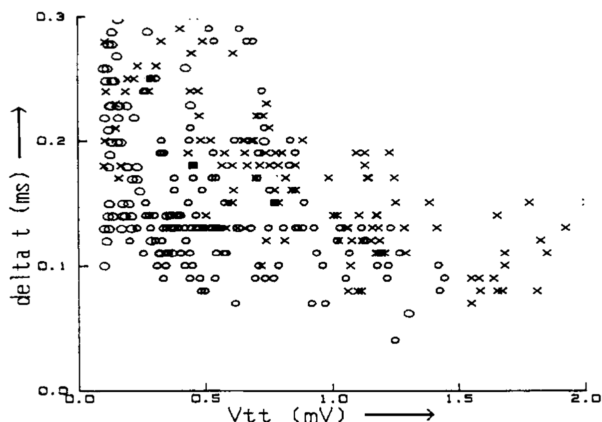


FIG. 4. Comparison of characteristics of SFAPs measured using two different techniques: Δt as a function of V_{tt}. Cross symbols indicate SFAPs rcorded with wire electrodes, circle symbols indicate SFAPs recorded with the multi-electrode.

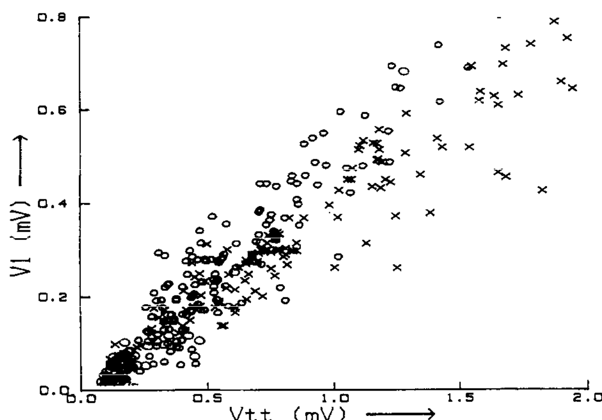
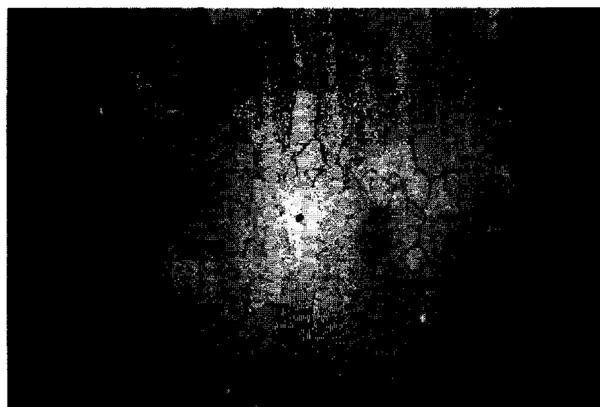
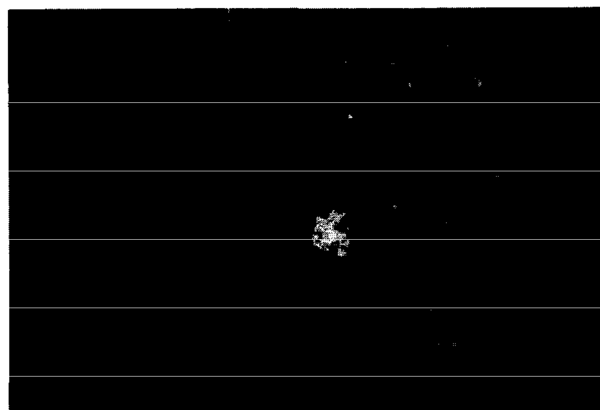


FIG. 5. Comparison of characteristics of measured SFAPs: V_1 as a function of V_{tt}. Cross symbols indicate SFAPs recorded with wire electrodes, circle symbols indicate SFAPs recorded with the multi-electrode.



(a)



(b)

FIG. 6. a, Fluorescence photograph of part of a cryosection.The lightly coloured fibre (indicated with a dot) is the one labelled with Lucifer Yellow.The bar represents 100 μm. **b,** Bright field reflection photograph of a cryosection. The silver deposit reflects the light and is clearly discernable from other non-metal debris. The active fibre is marked with an *. The bar represents 100 μm.

storage of the cross-sections at low temperature, the fluorescent dye remained mainly in the fibre despite the fact that no fixation was used. An example of a fluorescent active fibre is shown in Figure 6a. The active fibre was followed from slice to slice through the muscle until slices with silver deposits were found. Reliable fibre labelling was achieved in 15 out of 145 experiments (total number of experiments in the present study and that of Albers et al.[4]).

The silver deposit originating from one particular recording site was found in one or sometimes two adjacent slices. Its size varied between 50–500 μm^2 (Figure 6b). The positions of the silver deposits could reliably be found using a bright field microscope. Nine cases were tested to ascertain whether the silver deposits remained in position during sectioning of the muscle. For this purpose, after depositing the silver layers, the wires were carefully cut about 2 mm above the muscle surface. The remnants of the wires were left in the muscle. The sliced wire electrodes (being an additional indication of the recording position) could easily be found in the slices. Only in one of these cases was the silver deposition not close to the wire tip. This might have been caused by movement of the wire when cutting it. No evidence was found for possible shifting of the silver deposits during sectioning of the muscle.

Before each experiment all wire electrodes were

checked to see if silver layers were present on the tips. After every experiment the wires were checked again. In all observations the silver layer had disappeared after electrophoretic deposition (this was done if an acceptable SFAP had been recorded on that particular electrode, see the Methods section). In the case that no electrophoretic deposition was executed, the silver layer was still found at the tip of the electrode. The number of silver depositions found in the muscle was always equal to the number of deposits made.

In 22 recordings out of 15 experiments the distance between the active fibre and the recording site was obtained. Peak-to-peak amplitudes of SFAPs, related to their recording distances are given in Figure 7. In this figure a model result (reported earlier[18]) is also shown. Generally, but not always, V_{tt} of recorded SFAPS decreased with increasing recording distances, in agreement with model predictions. The absolute values of V_{tt} were much higher than predicted by the model. Figure 7 did not allow for the determination of a relation between peak-to-peak amplitudes and recording distances. The recordings used to compose Figure 7 had values of Δt and V_1 seen in Figures 4 and 5.

In cases where two or more SFAPs originating from the same active fibre were recorded in response to the same stimulus, the conduction velocity was obtained from the time interval and the longitudinal distance between two SFAPs. Unfortunately, this could be done in only seven experiments. Conduction velocities ranged from 3.4–8.5 m s^{-1}. The cross-sectional area of these seven active fibres ranged from 1700–3100 μm^2. For this small number of results, no relation could be shown between the area of the active fibre and conduction velocity.

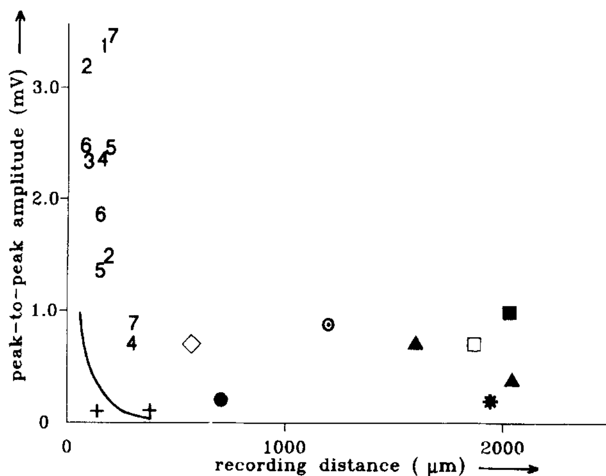


FIG. 7. V_{tt} of SFAPs, recorded with wire electrodes, and their corresponding recording distances. Data points, obtained from different experiments, are indicated by different markers. Data points marked by numbers 1–7 were reported previously[4]. The solid line indicates a model result reported previously[18].

Procedure 2: Multi-electrode Results

In multi-electrode results, no information concerning distances between the active fibre and the recording sites was available. Instead, the distance between the recording electrodes was accurately known. Thus the relative decline of V_{tt} as a function of the position of the recording electrode along the needle could be studied. Only registrations with detectable signals on at least four electrodes in the multi-electrode were considered. The highest peak-to-peak amplitude in a registration had to be at least ten times the rms value of the noise. Thirty-two registrations out of nine experiments fulfilled these criteria. Again, V_{tt} did not decrease with increasing recording distance in all cases. In 12 registrations more than one maximum (multiple maximum) was found in the plot of V_{tt} as a function of the electrode number. The other 20 registrations showed a smooth decline. Figure 8 shows examples of multiple maxima in four different experiments. Actual SFAPs corresponding to one of the multiple maxima in Figure 8 (experiment ben021b) were shown in Figure 3. These SFAPs exhibit normal shapes.

Reproducibility of SFAPs for a particular position of the active fibre was tested in a few instances when the micropipette stayed in the active fibre after stimulation. After stimulating the fibre a second time, peak-to-peak amplitudes of SFAPs could vary slightly, but no change was observed in the relative changes in the peak-to-peak amplitudes along the electrodes in the needle.

DISCUSSION

An expansion of the set of experimental data reported by Albers et al.[4] has been presented in this paper. A difference between the earlier study and the present one appears to be the range of recording distances: small recording distances ($r < 300$ µm) vs. larger distances (r up to 2 mm). The duration taken to search for high peak-to-peak amplitudes has been reduced, because the reliability of the marking procedure downgraded when it was started after a longer time.

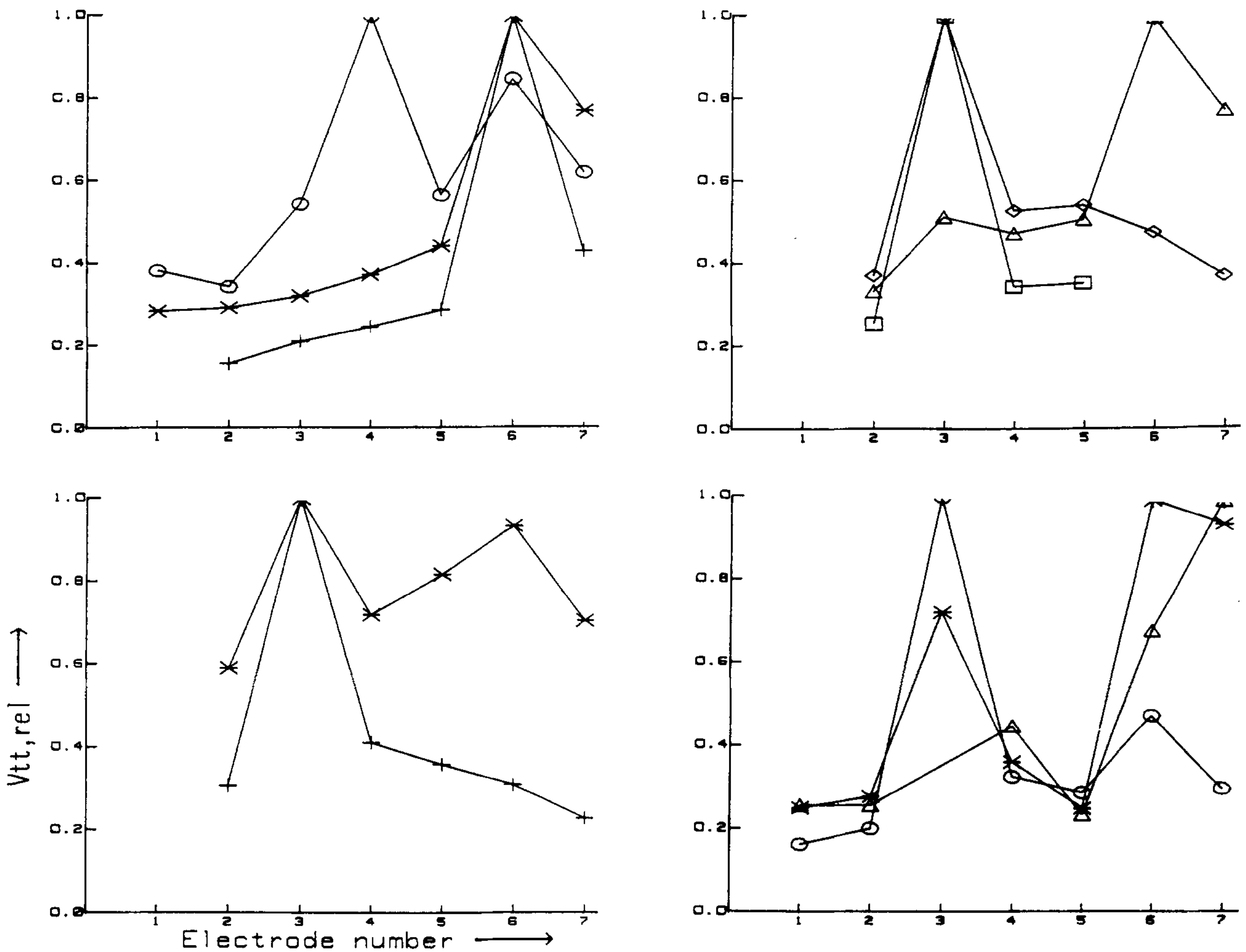


FIG. 8. Relative V_{tt} of SFAPs, recorded with the multi-electrode, as a function of the electrode number. For each experiment a separate figure is used, the codes of the experiments are written above the upper left corners and the ordinate is normalized using the maximal value of V_{tt} per registration. For each registration in a particular experiment, a different symbol is used. The electrode numbers are given in Figure 1. The maximal values per registration were: ben009, ○, 0.8 mV, *, 1.2 mV and +, 2.1 mV; ben017b, □, 0.8 mV, △, 1.3 mV and ◇, 1.3 mV; ben018, *, 0.8 mV, +, 1.1 mV; ben021b ○, 0.4 mV, *, 0.3 mV and △, 0.3 mV.

In the whole range theory seems to fail. In spite of the increased number of experiments the relation between V_{tt} and recording distance is still not clear. Variations in muscle structure seem to dominate normal volume conduction quite frequently. One should be aware of this phenomenon when performing single fibre electromyography. It has been carefully ascertained that the distance measured between the active fibre and the electrodes was accurate. The active fibre was located by its fluorescence and followed through successive cross-sections until the slices with the silver deposits were found. In three cases the identification procedures were independently checked by two persons. Their results were the same. Furthermore, the area of the active fibre was measured at different longitudinal positions. Its value was constant throughout the muscle, indicating that no mistakes were made while following the active fibre. Also, as reported in the Results section, it was checked that the silver deposits were not displaced by sectioning. Silver depositions were observed to be near, but generally detached from the wire surfaces. We feel confident that the measurement of recording distances in general has been correct.

In clinical results[8–10], a smooth decline of V_{tt} from a single maximum to both ends along a multi-electrode array was generally found, in contrast to our present results. Occasionally a multiple maximum in V_{tt} along the needle was reported[10].

Our present results indicate that high amplitudes on electrodes far away from the electrode with the highest SFAP amplitude were not related to motor unit background activity, as suggested by Gath and Stålberg[10]. The experimental protocol in the clinical setting differed from ours. In clinical recordings[8–10], the diameter of the multi-electrode needle was larger (> 400 μm). The diameter of our needle was 300 μm. In humans, muscle activity is evoked by voluntary contraction, not by stimulating one muscle fibre. In clinical trials the needle is moved through the muscle until a very high amplitude is found on one of the electrodes. Our multi-electrode remained at a constant position after insertion. By moving through the muscle, 'clinical' needles might have been surrounded by more extracellular fluid.

Gath and Stålberg[9] also compared their measurements with model results. A measured action potential (recorded in the direct neighbourhood of the active fibre) was transmitted through a filter simulating the low-pass characteristics of the muscle tissue. The authors reported a good agreement between the radial decline of peak-to-peak amplitudes of SFAPs experimentally found and the decline predicted by their model. However, characteristics of the low-pass filter were chosen quite arbitrarily with no link to morphology and biophysics.

In our experiments, upon inserting either the wire electrodes or the multi-electrode, it was ensured that the insertion depth of all electrodes was at least 1 mm. Furthermore, the position of the active fibre relative to the muscle surface was monitored. In most cases, the active fibre was at least 500 μm under the muscle surface. It was theoretically shown that in that case no significant influence of the muscle boundary upon V_{tt} was to be expected[18].

In muscle tissue, irregularities in conductivity occur due to the presence of blood vessels or connective tissue. In simulations a non-smooth decline of V_{tt} with recording distance was obtained by assuming the presence of geometric conductivity distortions[19]. Maximum deviations from a smooth decline were found when conductivity distortions were present in the neighbourhood of the active fibre or the recording electrodes[19]. Connective tissue layers in skeletal muscle gave rise to an increase of SFAP amplitudes up to about 40% compared to an undisturbed situation around the active fibre. Histological studies[4] showed connective tissue layers surrounding groups of about 10–40 muscle fibres in rat EDL muscle. The chance of having one or more connective tissue layers between the active fibre and the recording site is appreciable. This could explain a non-smooth function describing the decline of peak-to-peak amplitudes with recording distance. However, it cannot account for multiple local maxima in the V_{tt} curves.

It is very unlikely that branching of muscle fibres will clear up the occurrence of multiple maxima. In rat muscle it has been shown that only 1% of the muscle fibres were branched[5]. Furthermore, while following the active fibre through the muscle (Results section, procedure 1) we were aware of the possible branching of muscle fibres; nevertheless it was not observed.

The relatively high SFAP amplitudes at large radial distances are not understood. Such high V_{tt} values were found with both the wire electrodes and the multi-electrode (this study, and Refs. 4, 8 and 10). Higher predicted values for V_{tt} in model studies were obtained by assuming other parameters[3]. A very critical parameter is the extracellular volume fraction p. When decreasing it from 0.15 to 0.05 (which is a realistic variation) V_{tt} increases by a factor of 2.5 in the neighbourhood of the active fibre[3]. In previous model studies[17–19] a value of 0.10 was chosen for p. The value of the membrane capacitance is also critical[1]. However, varying those microscopic volume conduction parameters changes peak-to-peak amplitudes of SFAPs, especially close to the active fibre. At larger radial distances, V_{tt} curves remain virtually unchanged.

Variation in impedance of electrodes may slightly influence the decline of the peak-to-peak amplitude. Before each experiment the electrode surfaces are plated with a new layer of silver and the impedance of the electrodes therefore varies from experiment to experiment. A constant effect on the profiles of the amplitudes along the needle is out of the question. The frequency content of the signal determines the attenuation. Signals with relatively high frequencies are attenuated most, and it is likely that this is particularly the case for recordings close to the active fibre. Optimization of the transfer characteristics of the electrodes and the cable should contribute to an increase of V_{tt} and so particularly to the further enlargement of the difference between simulated and experimental amplitudes of SFAPs at small recording distances.

The shape of the SFAP is partly determined by its source function. Amplitudes of simulated SFAPs are up to a factor of 1.8 higher when originating from a fast source function, compared to a slow one[3]. With an actually measured transmembrane

current as a source function, SFAP amplitudes increase by about a factor of 2 in comparison to conventional source representations[20]. However, when assuming this more realistic source function in the model calculations, predicted V_{tt} values are still much too low, especially at large radial distances.

CONCLUSIONS

The relation between peak-to-peak amplitudes of volume conducted SFAPs and the positions of their corresponding recording sites is poorly understood in the *in vivo* situation. The most important differences between model and reality are the non-monotonic decline of peak-to-peak amplitudes with increasing recording distance, as well as the high amplitudes close to and far away from the source. Incorporation of non-regular and non-symmetric properties of muscle tissue in models does not remove these differences. The present results suggest that between the active fibre and the recording electrodes, conducting pathways exist that are not accounted for in volume conductor models. The data presented argue against interpreting amplitudes of SFAPs in terms of recording distances or pick up areas.

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