Transverse flow of middle-frequency alternating current, a new method for the study of cell rhythms in muscle fibres

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Abstract

Transverse flow of middle-frequency (5,000 c. p. s.) alternating current applied to a proximal nerve-free portion of frog sartorius muscle was found to be an appropriate method to elicit inherent spike rhythms in muscle fibre. An adequate compensation of the activating current artifact was achieved by means of an RC-bridge array. The primary effect of the m. f. current flow was a slowly rising, even, "reactive" depolarization. With a flat current rise, the increasing reactive depolarization after reaching threshold gave way to rhythmic spike activity (no accommodation). Two forms of repetitive spike activity were elicitable: trains of rapidly repeated spikes (50–290 p. s.) and series of spikes at low rate (4–8 p. s.). The difference in spike rate corresponds to a difference in the course of self-repolarization. Within the trains, the depolarization to the next spike occurred immediately after a one-stage, partial repolarization. Within the series, the repolarization occurred in two stages: a rapid stage followed by a slow one reaching approx. the level of the resting membrane potential.

Introduction

Alternating current applied to skeletal muscles evokes repetitive excitatory responses. It has been shown that at low frequencies (up to 300 c.p.s.) synchronism occurs between each cathodic current slope and the spike produced, a phenomenon in accordance with PFLÜGER's law. At somewhat higher frequencies (up to 500 c.p.s.), however, only each second cathodic slope is followed by a single response, because of the relative refractory period. At frequencies above 500 c.p.s. the law of synchronism no longer exists, the muscle fibres, following their own inherent rhythmicity, produce individual trains and/or series of repetitive responses.

BUCHANAN [7] presented the first systematic study of the higher alternating current frequencies just described and found that the primary effect of stimulation was a continuous state of local electric negativity, i.e., a depolarization of long duration. Many authors have since then confirmed this a.c.-dependent reduction of membrane potential on muscle fibres [11, 15, 19].

GILDEMEISTER [9] proposed the term "Mittelfrequenz" (middle-frequency, m.f.) for these higher frequencies of alternating current.

KUMAZAWA [12, 13] demonstrated on single muscle fibre that the permanent depolarization under the influence of these middle-frequency currents depends completely on the existence of sufficient extracellular Na^+-concentration and may hence be considered a primary membrane reaction. KUMAZAWA and WYSS [14] termed this membrane process "reactive depolarization".

The aim of the present investigation was to define the relation between the rate of the repetitive responses, representing the inherent rhythmicity of the muscle fibre, and the time-course of the reactive depolarization produced by gradually increasing m.f. alternating current of 5,000 c.p.s.

Method

The experimental technique was as described by KUMAZAWA [13] with, however, the addition of the following modifications:

1. In the ionic composition of the RINGER solution the $CaCl_2$ was 1.80 mMol per l (instead of 1.08). The "over night" solution did not contain bicarbonate but was buffered with NaH_2PO_4 0.85 + Na_2HPO_4 2.15 mMol per l. The same solution system was used for the first series of experiments (a: 1–44), but for the second (a: 45–100), a "Tris Buffer pH 7.4", obtained by mixing Trizma-HCl with Trizma-Base (Sigma® Chemical Company) at 8.0 mMol per l. No tubocurarine was added to the solutions.

2. Middle-frequency sine wave current of 5,000 c.p.s. instead of 20 kc.p.s. was used as carrier frequency. In contrast to KUMAZAWA's rectangular form of current pulses (amplitude at constant level), modulation of the amplitude was drop- or triangular-shaped. In the present experiments, an impulse generator [21] delivered the drop-shaped "bursts" of a.c.-cycles, the amplitude waxing within 7 ms to its maximum and waning within the next 35 ms to zero. This stimulus has been called middle-frequency impulsion (m.f.-impulsion, [21]). A linearly increasing current device [20] yielded the triangular-shaped m.f. current (termed "triangular m.f. current"), the amplitude rising at fast or slow rate until sudden current interruption.

3. As the muscle (sartorius of frog) was not curarized, transverse current flow was applied to the nerve-free proximal end, in the middle portion of which intracellular recording was arranged.

The m.f.-impulsions served as testing stimuli. They were used in the first part of each experiment in order to examine the degree of reliability of the experimental array and the grade of responsiveness of the muscle fibre to be investigated. In the second part the response of the fibre was obtained by applying the triangular m.f. current.

Results

The reaction of the muscle fibre membrane potential to gradually increasing m.f. current consists in a slowly increasing reactive depolarization, which, after reaching the spike threshold, generates trains or series of repeated spikes.

1. Membrane reaction to m.f.-impulsions

M.f.-impulsions (form and duration defined above) applied at subthreshold intensity produce a reactive depolarization process, the course of which is shown in fig. 1. Applied at just above-threshold, these m.f.-impulsions produce trains of 3–5 rapidly repeated spikes (fig. 1). It should be noted, that the summit of the reactive
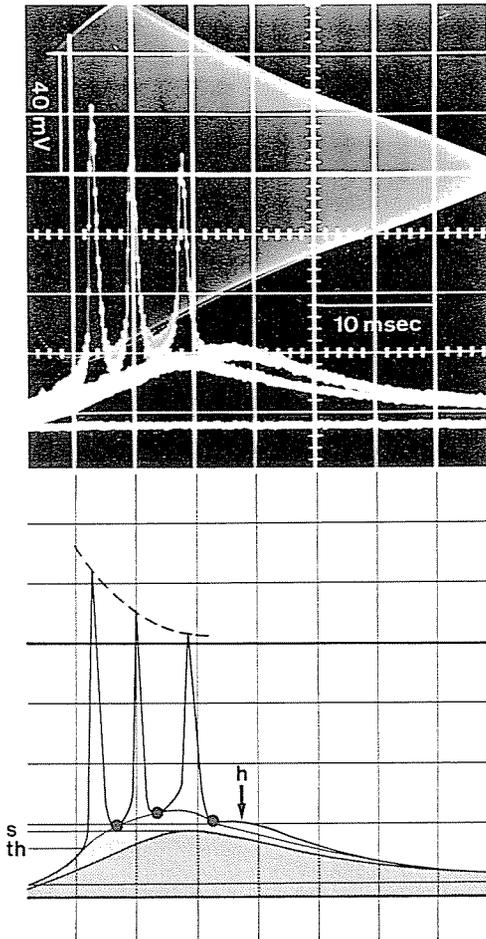

Fig. 1   The characteristic responses of the muscle fibre membrane to a subthreshold and a just-above-threshold m.f.-impulsion. The photograph (upper part of fig.) shows two original records on the same time axis (abscissa). The zero line of two m.f.-impulsions (above) coincides with the zero level of the two membrane potential reactions (below). In the drawing (lower part of fig.), the contourline of the dark stippled area represents the subthreshold reactive depolarization "wave", and the contourline of the light stippled area, the just-above-threshold reaction, i.e., the base-line of the train of 3 rapidly repeated spikes including their base-points. The slight hump (h) marks the failure of the last spike. Note that the summit (s) of the subthreshold depolarization "wave" exceeds the membrane threshold (th) of the first spike.

depolarization process (which remains just under the threshold of spike generation) exceeds the level of the membrane potential at which an m.f.-impulse at just above-threshold intensity elicits its first propagated spike. Within the train, the spikes follow one another at increasing or decreasing rate (between 250 and 290 p.s.), the spike amplitude decreases, and the last spike may sometimes fail to reach the zero line, thus becoming abortive. Sometimes a slight hump appearing early in the re-polarization curve, marks the failure of the last spike.

With reference to the time-course of the m.f.-impulse, the appearance of the first spike and the whole following train falls within the declining phase of the m.f.-impulse.

With reference to the time-course of the reactive depolarization process, the first spike in most cases emerges from the progressive, seldom from the regressive part of the ascent. The fast repolarization of the first and following spikes stops suddenly at a base-point (fig. 1). Each base-point within the train is the onset of a new progressive depolarization which in turn induces a fresh spike. Each following spike resembles the preceding one in shape, but is somewhat less high. The repolarization of the last (sometimes abortive) spike, however, after reaching the base-point continues more slowly, and is at times preceded by an intermediary depolarization hump.

Fig. 1 shows that a continuous line can be drawn through all the base-points of the spike train (base-line). This base-line joins the local reactive depolarization process leading to the first spike to the slow repolarization process following the last spike. The whole line thus follows the course of the reactive depolarization process ob-tained with the subthreshold m.f.-impulse, only that it is steeper and higher (ap-prox. 1,500 instead of 700 mV p.s. and 45 instead of 20 mV). Spikes can emerge as long as the line of the reactive depolarization process rises.
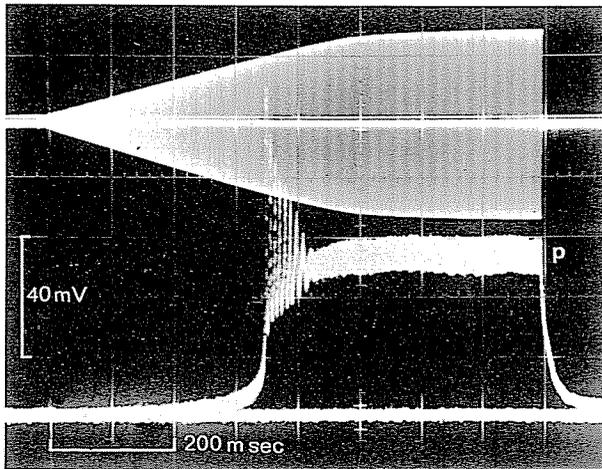

Fig. 2   Train of 8–9 rapidly repeated spikes elicited by a triangular m.f. current (rising first linearly, then regressively). Note the rise of the base-line continuing into a more or less horizontal plateau (p), and note the decrease of the spike height.

The rise of the base-line and the concomitant decrease of the spike height reduce the spike amplitude in such a manner that the amplitude reaches zero towards the end of the train. This occurs at a limit height of depolarization which corresponds to about one half of the resting potential.

2. Membrane reaction to triangular m.f. current

Under the influence of a triangular m.f. current the membrane potential remains at resting level until strength-threshold is reached. Further current rise provokes a progressively growing reactive depolarization which gives way to the spike train (fig. 2). According to the steepness of the linear current rise, the latency time of the first spike in these experiments ranges from about 100 ms to several min. The spike trains resemble those elicited by m.f.-impulsions. The base-line, however, gives way to a more or less horizontal plateau at about half membrane potential, in spite of the continuing current rise. With triangular current rise, therefore, the base-line of the spike train always reaches the level of depolarization at which the spike amplitude decreases to zero.

a) First spike latency times not exceeding one sec

Within latency times up to one sec duration, the time-course of reactive depolarization and hence of the base-line with its train of rapidly repeated spikes, depends on the steepness of the m.f. current rise. With decreasing rate of current rise the base-line also rises more slowly, i.e., the slope of the tangent through the inflexion of the base-line decreases too. The rate of the rapidly repeated spikes also depends on the slope of the base-line. The flatter the slope the lower the spike rate, the latter ranging from about 50 to 160 spikes p.s.

Whatever the latency time, the tangent slope is different between individual muscle fibres. A systematic relation between the tangent slope and the latency time of the muscle fibres examined exists only for the lowest tangent slope values. The slope/latency curve as shown in fig. 3 therefore only passes through these lowest tangent slope values. With increasing latency time, the curve falls from the highest slope values of 4,000–5,000 mV p.s. (obtained with the m.f.-impulsions) first steeply then regressively, approaching lowest slope value of 70 mV p.s. at approx. one sec latency time. With still lower rates of current rise, latency time increases far beyond one sec, reactive depolarization maintaining its lowest slope. This lowest slope of the base-line was, in every experiment, the basis of at least one spike of full amplitude.

b) First spike latency times exceeding one sec

By using m.f. currents of still slower rate of rise with first spike latency times exceeding one sec, another type of repetitive spike response can be observed, namely, a train of rapidly repeated spikes as described above, during which, however, an unexpected sudden change may occur. The rapid spike repolarization, instead of ceasing at the base-line, continues into a slow repolarization which reaches a *second*
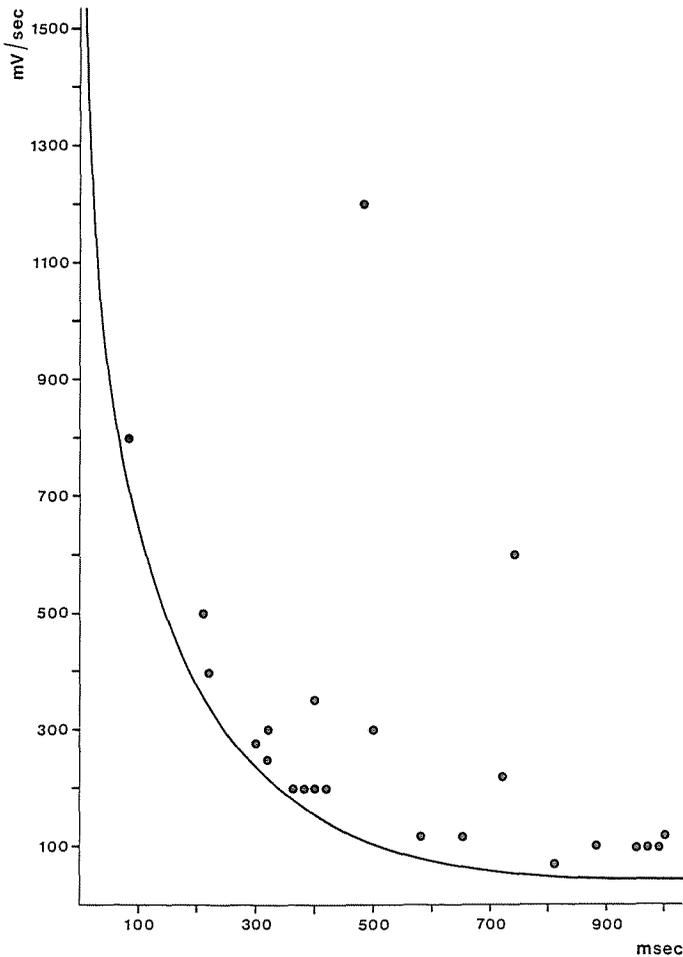
Fig. 3   Tangent slope values (mV p.s., ordinate) versus first spike latency times (ms, abscissa). Number of experiments: 23. The slope/latency curve shows the characteristic relation only for the lowest tangent slope values. Note that with increasing latency times the curve approaches the lowest value of 70 mV p.s., at approx. one s latency time.

base-point (fig. 4) lying just above the normal resting membrane potential level. The transition from rapid to slow repolarization may be marked by a hump in form of an intermediate – but short – steady state, "half-way" depolarization, for which the term "mini-plateau" is proposed. This *two-stage* type of *repolarization* is always followed by a spike of almost full amplitude. Because of the longer duration of the slower additional repolarization, the interval between the two spikes is considerably increased, ranging between 120 and 250 ms. Within a phase of high-rate activity, a single two-stage repolarization divides the train into two parts (fig. 4). The reiter-
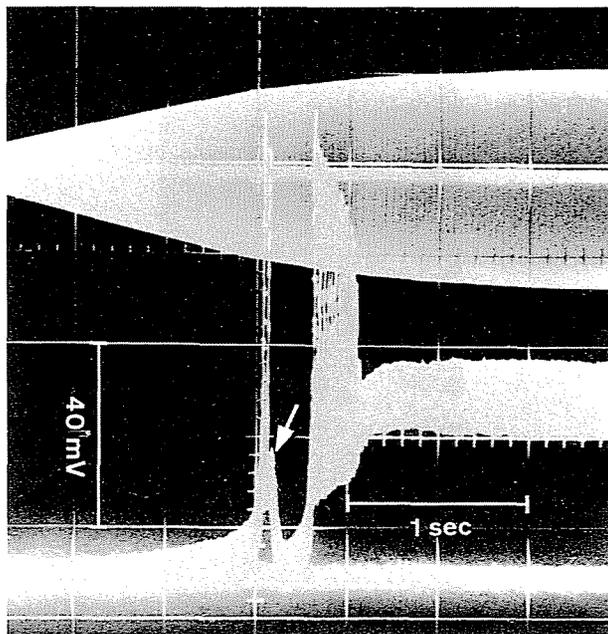
Fig. 4   A single two-stage type of spike repolarization closes the first part of train of rapidly repeated spikes. The second part, after an interval, is opened by a spike of almost full amplitude. The arrow marks the hump between the two stages of repolarization.

ation of the two-stage repolarization after each spike during repetitive activity results in an unbroken spike *series* at a low rate ranging from 8–4 p.s. (fig. 5). This repetitive fibre activity of low rate, however, occurs seldom (6 out of 165 experiments). The most appropriate stimulus in order to elicit a two-stage type of repolarization appears to be a m.f. current rise of intermediate slope with first spike latency time of 1 to 14 sec.

Discussion

The main advantage of the method used in these experiments is the adequate compensation of the activating current artifact. By means of the RC-bridge technique the current applied was prevented from flowing between the recording (intracellular) and indifferent (Ag-AgCl-plate in the bath) electrodes. A symmetrical array of the stimulating electrodes (bipolar) with regard to the derivating electrodes (unipolar) facilitates the compensation. This technique permits registration of even slight changes of the membrane potential, whether slow or fast, during m.f. current flow of several min duration. Interference with passive electrical changes due to the spread of current applied can thus be avoided. Unless this compensation technique is used, gradual changes of the membrane potential only appear as mean variation
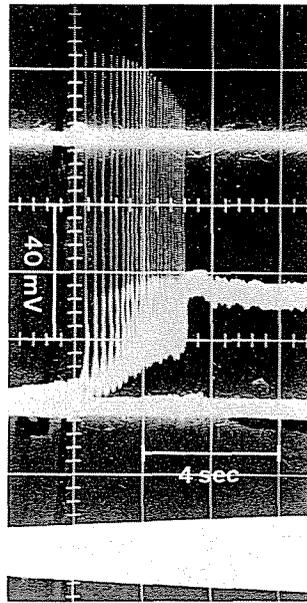
Fig. 5   A characteristic series of 25 spikes at a low rate (4–8 p.s.), elicited by an intermediate slope of m.f. current rise (latency time: 14 s). The repolarization of each spike occurs in two stages.

of the middle line of the alternating voltage recorded (e.g. as "mean depolarisation": [6, 15, 16]).

The primary effect of the m.f. transverse current flow is a reactive depolarization [14]. In contrast to the local response [2, 10] – which as a transient depolarization wave of about 3–4 ms follows a *single* alternating current cycle or a *single* direct current pulse – the reactive depolarization is a gradual process, which arises during the course of several cycles of 5,000 p.s. The even-rising reactive depolarization never shows any periodic regularity synchronous with the a.c. frequency.

The appearance of the reactive depolarization curve depends on the sub- or above-threshold intensity of m.f. current applied: In the first case, the depolarization is a single depolarizing variation and in the second case it is the base-line of a train of rapidly repeated spikes. These two forms of reactive depolarization are the product of a membrane inherent process. The final step of the latter is an increased Na^+-permeability, because any form of reactive depolarization depends entirely on the extracellular Na^+ ions. In a Na^+-free milieu no active and no physical depolarization is detectable under m.f. current flow. There is no reason to doubt that this reactive depolarization is similar to, if not identical with, the "intrinsic" depolarization encountered by OOYAMA and WRIGHT [17] on single RANVIER node of frog nerve membrane in a state of "low anodal opening threshold" [22, p.18].

In order to obtain a reactive depolarization, an increasing m.f. current intensity should be applied linearly (triangular m.f. current) or regressively (m.f.-impulsion).

When the maximum current intensity is reached within a few ms (rectangular or drop-shaped m.f. current), the development of the reactive depolarization is retarded and a characteristic time-lag of several ms between the moment of current maximum and reactive depolarization maximum occurs. Under a steady state m.f. current flow, however, the reactive depolarization after passing its maximum returns more or less slowly to zero.

The spike train elicited by a steep increase of reactive depolarization is short and its spike rate is high. The spike train is short because of the rapid, steep rise of the reactive depolarization, and the spike rate is high because the steepness of the increasing reactive depolarization determines the rate of the spike generation. All repetitive spike activity is stopped during the phase of plateau depolarization.

The slowest slope of the base-line of about 70 mV p.s. and thus spike train belonging to it, does not occur until the m.f. current reaches threshold intensity. The latter always remains the same, whatever the duration of the latency time may be. Thus, no accommodation occurs, in contrast to stimulation with triangular direct current rise [18]. Each triangular m.f. current rise, therefore, elicits a spike train, irrespective of the flatness of the m.f. current rise.

The use of a delayed m.f. current rise is an adequate method to provoke repetitive muscle fibre activity of long duration. The activated fibre membrane, however, generates spike rhythms, which are in no relation to the a.c. frequency of the stimulating m.f. current, and take the form of *trains* of rapidly repeated spikes (50–290 spikes p.s.) and/or *series* at low rate (4–8 spikes p.s.), as previous and present works have revealed. The difference between the two rhythmic activities lies in the course and the depth of the spike *repolarization*. The repolarization of the first, well-known type of rhythmic activity stops at a base-point which corresponds to the reactive, *local* depolarization. The spike rate is high because of the speed of the repolarization and the immediate transition of the latter into the following progressive depolarization. The repolarization of the second type of rhythmic activity occurs in a rapid step followed by a slow one. The *mini-plateau* which lies at the level of the base-line separates these two steps. The slow repolarization after the mini-plateau almost reaches the normal resting potential level in spite of the ongoing m.f. current rise! The spikes of this second rhythmic activity follow one another at a low rate because of the slow and almost complete repolarization. In contrast to the spike *trains* which end when the base-line has reached the plateau potential, the duration of the spike series are not predictable.

Few methods besides the m.f. current-flow produce local depolarization eliciting trains or series of repeated spikes. Thus ADRIAN and GELFAN [1] obtained such results with hypotonic extracellular milieu, FALK and LANDA [8] by replacing the chloride ion with a non-permeating anion and BENOIT, CORABOEUF and ETHENS-PERGER [4] as well as BROMM and SIMON [6] by depressing physically the membrane potential by pulses of constant current. All these methods show that each "wave" of local depolarization, irrespective of the stimulus used, evokes a train of rapidly repeated spikes; the observed spike rates are always in the range found in the present investigation. They are all, however, less adequate than the m.f.

current-flow method because when using them either the extracellular milieu must be chemically changed or the membrane potential physically depressed.

The time-course of the membrane potential change belonging to the slow fibre rhythm, i.e., series of rates of 4–8 spikes p.s., does not appear to have been previously analysed using electrophysiological methods. Only two reports describe repetitive mechanical muscle activity at a slow rate: BIEDERMANN [5] analysing the closing tetanus has observed a rhythmic muscle activity of about 2 p.s. and BENOIT and COPPEE [3] stimulating the muscle with direct current pulses found rhythmic muscular contractions at a rate of 1–3 p.s.

The long-lasting active lowering of the muscle fibre resting potential which characteristically does not exceed half membrane resting potential, has been observed by STEN-KNUDSEN [19], KUMAZAWA [12], MASHIMA and WASHIO [15] and by BROMM and SIMON [6]. No report, however, deals with the relation between the time-course of the rising depolarization until plateau level and the spike rhythms evoked.

The rising course of the reactive depolarization, i.e., the increasing sodium conductance of the stimulated membrane, is the cause of the rhythmically appearing spikes. This active potential change corresponds to what has been termed a generator potential. The fall of the membrane potential, however, inevitably provokes an inactivation of the sodium transport system. This inactivation process, along with the increasing sodium conductance, accounts for the two following phenomena: (a) The limited height of the reactive depolarization, and this in spite of the continuing m.f. current rise, and (b) the decrease of the amplitudes of the spikes, which lose overshoot during the train according to the rise of the reactive depolarization, i.e., the base-line.

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Zusammenfassung

Der proximale, nervenfreie Teil von exzidierten Musculi sartorii einheimischer Frösche wurde mit mittelfrequentem Wechselstrom (MF-Strom) von 5 kHz quer durchströmt. Das Membranpotential einer einzelnen Muskelfaser wurde in der Mitte des Durchströmungsbereiches zwischen den beiden, einander gegenüberliegenden Mittelfrequenz-Aktivierungselektroden mittels intrazellulärer Mikro-

elektrode abgeleitet. Das Reizartefakt wurde über eine symmetrische Widerstands-Kapazitätsbrücke kompensiert, damit der zeitliche Verlauf des Membranpotentials während der Einwirkung des MF-Stromes genauestens registriert werden konnte. Zur Aktivierung wurden zwei in verschiedener Weise amplitudenmodulierte MF-Ströme verwendet: *MF-Impulse* und *MF-Dreiecksströme*. Die *MF-Impulse* mit quasi tropfenförmiger Umhüllung erreichten nach einer fest eingestellten *Anstiegszeit* von 7 ms den Maximalwert, um anschliessend innert 35 ms wieder abzufallen. Demgegenüber nahmen die Amplituden der *MF-Dreiecksströme* mit einstellbarer *Steilheit* lediglich kontinuierlich zu.

Die primäre Wirkung dieser MF-Ströme längerer Dauer war das Auftreten einer schon früher als reaktiv bezeichneten, lokal bleibenden Depolarisation, deren Verlauf keinerlei Schwankungen im Rhythmus der einwirkenden MF-Stromperioden zeigte. Mit dem Überschreiten einer gewissen Schwelle ging diese reaktive Depolarisierung in eine repetierende Spike-Aktivität über, wobei zwei ganz verschiedene Spike-Rhythmen beobachtet werden konnten: ein rascher Rhythmus von 50 bis 290 Spikes pro sec und ein langsamer von lediglich 4 bis 8 Spikes pro sec. Die beiden Rhythmusformen unterschieden sich durch einen verschiedenartigen Repolarisierungsverlauf der einzelnen Spikes. Beim *raschen Spike-Rhythmus* repolarisierte sich die Membran nach dem Overshoot mit konstanter, grosser Geschwindigkeit lediglich bis zu einem sogenannten *Basispunkt*, von welchem aus eine erneute progressive Depolarisierung unmittelbar zum Auftreten des nächsten Spikes führte. Dieser Übergang von der schnellen Repolarisierung in die im Basispunkt unmittelbar anschliessende Depolarisierung wiederholte sich im Spike-Intervall innerhalb einer ganzen Serie sich rasch folgender Spikes in gleichartiger charakteristischer Weise. Beim *langsamen Spike-Rhythmus* schloss sich eine bedeutend langsamere Repolarisationsphase an den Basispunkt an. Durch eine solche zweistufige Repolarisation vermochte sich die Membran fast vollständig zu repolarisieren, bevor erneute Depolarisierung zum nachfolgenden Spike führte. Zwischen der schnellen und der langsamen Repolarisationsphase konnte ein mehr oder weniger ausgeprägter Depolarisationshöcker auftreten. Diese zweistufige Repolarisierungsart ist die bisher in der Literatur nicht beschriebene Grundlage des langsamen Muskelfaser-Rhythmus.

Die Verbindungslinie zwischen den innerhalb einer Spike-Serie sich folgenden Basispunkten, die *Basislinie*, war in allen Fällen S-förmig. Der Anfang der Basislinie war die kontinuierliche Fortsetzung der reaktiven Depolarisierung, und das Ende ging entweder in die letzte, langsame Phase der Repolarisation über (MF-Impulse) oder aber in eine sogenannte plateauförmige Dauerdepolarisation auf ungefähr dem halben Wert des Ruhe-Membranpotentials (MF-Dreiecksströme). Mit dem Übergang in die plateauförmige Dauerdepolarisation («Plateau») endete spätestens die Spike-Aktivität.

Die Aktivierung von Muskelfasern an umschriebener Stelle mit mittelfrequentem Wechselstrom ist eine geeignete Methode, um zwei verschiedene spontane Zellrhythmen von Muskelfasern in Erscheinung treten zu lassen.