Biol. Cybern. 66, 253–259 (1992)

Biological Cybernetics

Excitability of single firing human motoneurones to single and repetitive stimulation (experiment and model)

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Received April 8, 1991/Accepted in revised form September 10, 1991

Abstract. The activity of single motoneurones of m. *flexor carpi ulnaris* (FCU) was investigated by recording their motor unit (MU) action potentials during weak and moderate voluntary muscle contractions. The MU firing rate range was 4.5–15 imp/s. The excitability of motoneurones was tested with a number of single stimuli eliciting a monosynaptic H-reflex of low amplitude. Two different indices were defined which relate to motoneuronal excitability: the *response index* – the ratio of the number of responses of a motoneurone to the total number of stimuli, and the *response time* – the time after the last background MU discharge at which motoneurone is ready to respond to the excitatory volley. Both the response index and the response time were determined for single motoneurones at different levels of background activity. In the lower range of firing rates, the response index for all motoneurones decreased when increasing the firing rate, but it remained constant in the higher rate range. This kind of response seems to be a typical motoneuronal response to the stimulation with single stimuli. The data on the response time were used to study the excitability of the same single motoneurones to computer simulated repetitive stimulation (stimulation rate 40–100 imp/s). In this case, the excitability of each motoneurone was determined as an increment of its firing rate in response to the stimulation. For the lower firing rate range, the excitability for all motoneurones also decreased when the firing rates increased whereas a variety of slopes was obtained in the higher rate range. The results of our experiments and their computer simulation allow us to suggest a possible interrelation between the excitability of firing motoneurones and their interspike membrane potential trajectories.

1 Introduction

The response of a firing motoneurone to additional synaptic inflow is substantially influenced by the periodic changes of its state within the interspike interval (ISI) after each discharge. Therefore the excitability of a motoneurone should be dependent on its background firing rate. There are some other rate-dependent characteristics of motoneuronal activity, such as ISI variability and distribution. Person and Kudina (1972) and Khushivadze (1979) presented data indicating that during voluntary contractions of fast and slow muscles these characteristics changed for each motoneurone around certain transient values of the firing rate. The range of ISI lengths at which this transition occurred corresponded to the range of afterhyporpolarization (AHP) duration determined in analogical muscles of animals (Eccless et al. 1958). For convenience, the firing rates below and above this transient value will be further referred to as "lower" and "higher" rates, respectively.

In the present paper, we intend to concentrate on the particular case of motoneuronal excitability to the additional inflow which produces in a motoneurone discrete excitatory postsynaptic potentials (EPSPs). In this respect we can refer to a few human and animal studies.

The excitability of firing motoneurones was determined during voluntary contractions of human muscles by studying the probability of motor unit (MU) responses to the number of consecutive single stimuli which were applied to the Ia afferents. The relationship between the excitability and the firing rate was investigated by Kudina (1987, 1988); and Miles et al. (1989) in m. *triceps surae* (TS) and by Kudina and Churikova (1987) in m. *flexor capri ulnaris* (FCU). In the lower rate range, the excitability in both muscles decreased when increasing the firing rate. In the higher rate range the excitability in TS remained fairly constant whereas in FCU it decreased further but with a slightly lower slope. These results were in general in agreement with more fragmentary data obtained earlier by Ashby and Zilm (1982b) in m. *tibialis anterior* (TA) and by Miles et al. (1987) in m. *masseter*.

The influence of repetitive excitatory stimulation in humans cannot be studied since a monosynaptic response to consecutive stimuli applied to the nerve would be obscured by the long lasting side effects of the previous stimuli. Therefore we can refer only to a few experimental studies performed on animals. Shapovalov (1972, 1975) investigated the influence of repetitive stimulation of descending monosynaptic pathways on single cat motoneurones which were firing in response to intracellularly injected electric current. The stimulation rate varied from 10 to 100 imp/s. The aim of Shapovalov's experiments was not to investigate motoneuronal excitability explicitly. Nevertheless, after recalculating of his results, it was possible to determine motoneuronal excitability in terms of a firing rate increment produced by the repetitive stimulation. In one series of his experiments the motoneuronal excitability increased when the background firing rate grew, but in the other series it remained virtually constant.

Thus, it remains unclear whether there is any consistent relationship between the excitability and the background firing rate of a firing motoneurone. The aim of this paper is to analyse in more detail the factors influencing the motoneuronal excitability and to provide better understanding of the reasons for the discrepancies in the results of the above mentioned experiments. With this purpose in view, we studied in human m. FCU the individual excitability of motoneurones to both single and repetitive stimulation. The excitability of each motoneurone to single stimuli was experimentally determined by recording its muscle unit potentials. The results of the experiments became the starting point for stochastic computer modelling thus making it possible to determine the excitability of the same motoneurones to repetitive stimulation.

2 Motoneuronal excitability to single stimulation

2.1 Experimental methods

Single MU potentials during slight or moderate isometric contractions of the m. FCU were recorded. Single stimuli that evoked weak global *H*-reflex (about 5% of the maximum *H*-response) were applied at random to the n. *ulnaris* and then the MU responses were studied. In each test, the background firing rate for each MU was calculated as a reciprocal of its mean ISI duration which had been determined from the duration of 4–5 ISIs measured prior to the stimulus. The investigated firing rates varied from 4.5 to 15.0 imp/s. During the experiment a human subject was typically able (by varying muscle contraction force) to change the mean firing rate of a single MU by 6–8 imp/s. During one experimental session 300–500 testing stimuli were applied.

The results obtained for each single MU were grouped according to their mean background firing rate. Within each group each test was categorized according to the time of the arrival of an excitatory volley to a motoneurone with respect to the last background spike (to 10 ms wide bins). For each bin a response index (*RI*) was calculated to be a ratio of a number of responses to the total number of respective excitatory volleys. In addition, for each mean background firing rate the motoneuronal excitability was determined in terms of the cumulative response index RI_c calculated as a ratio of the total number of responses to the total number of stimuli. For more details concerning the experimental procedure see Kudina (1988); Kudina and Churikova (1987).

It is obvious that the reliability of the results of such data processing would essentially depend on the number of data in each bin. Therefore, from the total number of 55 motoneurones tested and used to obtain motoneuronal population response (Kudina and Churikova 1987), we were able to choose only 5 (for which sufficient experimental material was collected) for the present single motoneurone study. Other results showed similar but more fragmentary data.

The interpretation of the experimental results was based on the simple scheme of interaction between an EPSP and interspike membrane potential trajectory of background MU firing (Fig. 1A). Similar approach was also applied by many other authors, e.g. Ashby and Zilm (1982a, b); Fetz and Gustafsson (1983); Matthews (1984); and Miles et al. (1989). For a given length of ISI and EPSP amplitude, this scheme corresponds to the stepwise dependence of the response probability on the time after the last spike, as shown in Fig. 1B. The time t_r after which the motoneurone begins to respond to the EPSP will be further called *response time*. This value is also related to the excitability since the motoneurones with lower t_r values respond to the stimulus during a greater part of their ISIs than the other ones (cf. Fig. 1A).

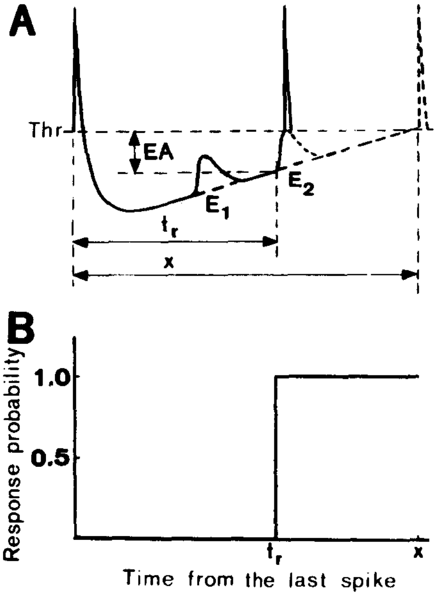

Fig. 1. **A** A schematic representation of an interaction between EPSPs (E_1, E_2) and the trajectory of motoneurone membrane potential within a single ISI of background activity: Thr – threshold; *EA* – EPSP amplitude; *x* – ISI duration; t_r – response time; **B** Response probability corresponding to **A**

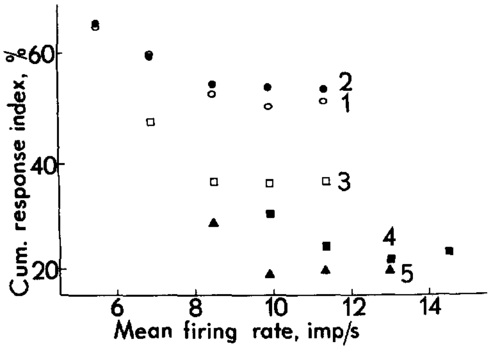

Fig. 2. Cumulative response indices plotted vs mean firing rate for motoneurones # 1–5

2.2 *Experimental results*

Figure 2 shows the dependence of cumulative response index RI_c on the background firing rate R_x for all the 5 motoneurones. It can be seen that the $RI_c(R_x)$ curves for individual motoneurones are scattered over the plot but their character is similar. There is always an inverse proportionality between the RI_c and the firing rate in the range of lower firing rates and a plateau in the higher rate range. The curves are also similar to the analogous dependence obtained for the population of MUs from TC (Kudina 1988) but different from the population curve for FCU (Kudina and Churikova 1987). This difference is probably due to the higher scatter of curves for individual MUs in FCU than in TC.

Figure 3 shows a typical example of the experimental dependence of RI on the time of the excitatory volley arrival within ISI for different firing rates (the motoneurone # 2). The shapes of these curves differ from a model one shown in Fig. 1B: each curve has a certain time range, when $0 < RI < 1$. This reflects the variability of the response time which may be brought about by some instability of the firing threshold and the EPSP amplitude. A more significant factor is probably the noisy interspike membrane potential trajectory which is due to a variation in the on-going synaptic inflow which results also in the natural variability of the ISIs of the background firing.

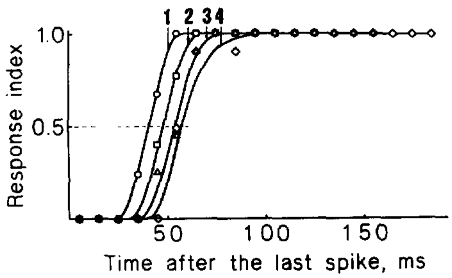

Fig. 3. Experimental response probabilities for motoneurone # 2 calculated as response indices for consecutive values of time after the last background spike. Single curves correspond to the following ranges of firing rates: 1 (circles) – 10.5–12.0 imp/s; 2 (squares) – 9.0–10.5 imp/s; 3 (triangles) – 7.5–9.0 imp/s; 4 (diamonds) – 6.0–7.5 imp/s

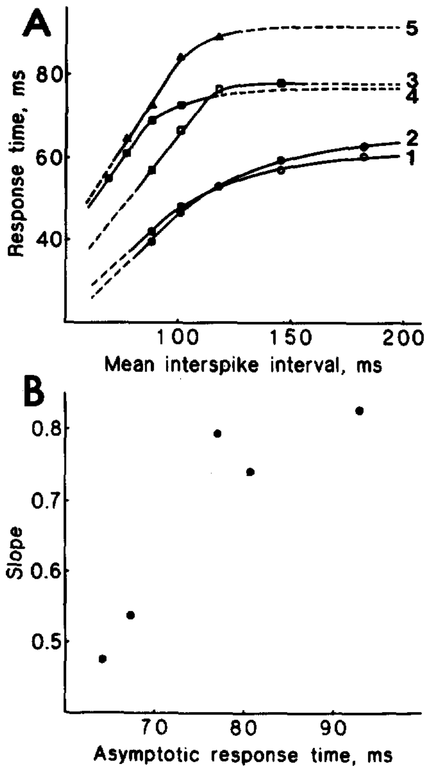

Fig. 4A,B. Characteristics of responses to stimulation of the motoneurones investigated (# 1–5): **A** Dependence of response time on mean ISI length; **B** Correlation between asymptotic value, t_{rs} and slope, a (cf. form. 1)

Therefore the motoneuronal response time t_r for each background firing rate was determined from the corresponding experimental curve as the time after the last background spike when $RI = 0.5$. The response time found out in this way corresponded to the actual value of response time for a mean ISI length.

Figure 4A shows the so determined response times (points) plotted against mean ISIs for the 5 motoneurones which were fully analysed. All the dependences have similar shapes. In the range of shorter ISIs the response time increases along with the ISI and this dependence may be regarded as linear. For longer ISIs this increase becomes slower, the dependence takes the form of the curve that seems to be heading towards a plateau. The ISI value at which this transition occurs can be only roughly estimated. Nevertheless, there are noticeable differences in the ISI transition values among those curves. The curves differ from one another also with respect to absolute values of t_r and the slopes of their linear parts. There is a tendency to a positive correlation between the position of a curve with respect to t_r axis and the slope of its linear part, as shown in Fig. 4B.

2.3 *The implications of possible membrane potential trajectories for the $t_r(\bar{x})$ function*

The function $t_r(\bar{x})$ reflects the ability of a firing motoneurone to respond to a stimulation. It seemed inter-

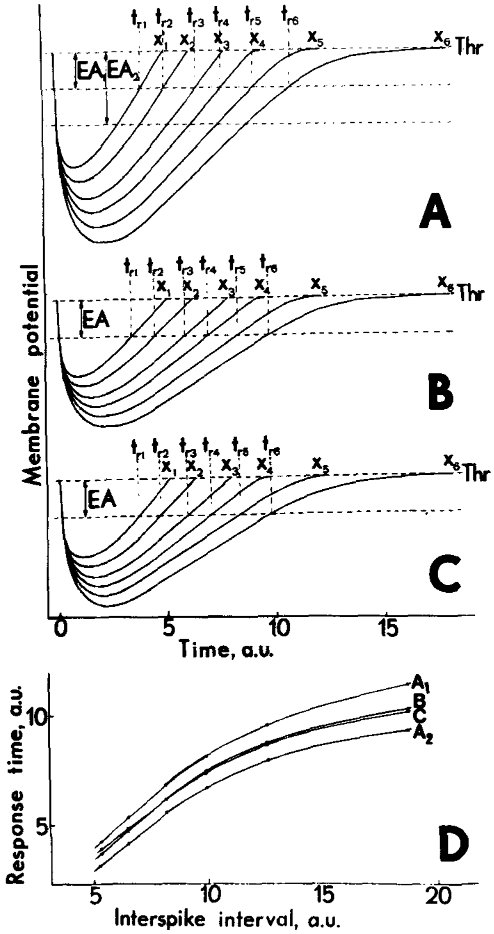

Fig. 5A–D. Schematic representation of a correspondence between interspike membrane potential trajectories and dependences of response time on ISI length: **A**, **B** trajectories of different depth; **B**, **C** trajectories of different rates of ramp divergence (**B**, less divergent, **C**, more divergent); **D** – $t_r(\bar{x})$ corresponding to **A**, **B** and **C** (A_1, A_2 – curves for different EPSP amplitudes). *Symbols*: Thr – threshold; $\bar{x}_i$ – mean ISIs; t_{ri} – response times; *EA*, EA_i – EPSP amplitudes

esting to analyse which factors may be responsible for differences in this function for different motoneurones.

Figure 5A–C shows schematic representations of the possible membrane potential trajectories for different ISIs. As experimental and model investigations have shown (e.g. Baldissera and Gustafsson 1974; Kostyukov et al. 1981), the rising phases of trajectories ("ramps") for shorter intervals are almost linear and divergent. When the ISI length approaches the AHP duration, the ramps become more "exponential". As shown by simple geometrical constructions in Fig. 5, this may account for the typical shape of the $t_r(\bar{x})$ relationship (cf. Fig. 4A). The linear part of this relationship corresponds to the range of ISIs in which the tranjectory may be regarded as linear. The values around which the character of the curves changes, should represent a very rough estimate of AHP duration. These estimates are close to the range of AHP durations recently experimentally determined in human FCU by Kudina et al. (1989).

For the given EPSP amplitude the position of $t_r(\bar{x})$ with respect to the t_r axis is dependent on the trajectory depth (cf. Fig. 5D, curves A_1 and B). The slope of the linear part of $t_r(\bar{x})$ reflects the degree of the divergence between the ramp phases of the membrane potential trajectories at different firing rates (curves B and C).

The position of $t_r(\bar{x})$ with respect to the t_r axis depends also on the amplitude of the EPSP (cf. Fig. 5D, curves A_1 and A_2). In this case, the slopes of the linear part and the maximum values of t_r for both curves are positively correlated as it was shown in the experiment (cf. Fig. 4B).

3 Motoneuronal excitability to the repetitive stimulation

3.1 Modelling method

For the purpose of modelling, each dependence from Fig. 4A was approximated by the following formula

$$t_r = \begin{cases} a\bar{x} + b & \text{for } \bar{x} \le x_t \\ t_{rs}(1 - \exp(-c(\bar{x} - x_0))) & \text{for } \bar{x} > x_t \end{cases} \qquad (1)$$

where $\bar{x}$ was a mean ISI, a – the slope coefficient and b – the intercept of the linear part of a curve. x_t was the point of transition from a linear to a curvilinear function. The curvilinear part of the formula represented a function which gradually approached a plateau limited by the value t_{rs}. All the coefficients a, b, t_{rs}, c, x_0 and x_t were chosen for each single motoneurone so as to obtain the best visual fit with the experimental data. The curves computed according to this formula are shown as lines in the Fig. 4A.

The modelling was performed on a computer IBM PC-AT. In each simulation cycle a time sequence of output spikes was obtained by the following procedure (see Fig. 6):

1. The times of occurrence of consecutive spikes of background activity (trace X) were computed according to the normal distribution of ISIs with parameters $\bar{x}$ (mean) and SD_x (standard deviation). For each motoneurone, the values of $\bar{x}$ were taken from its experimental range of ISIs, and SD_x varied from 5 to 35 ms depending on $\bar{x}$ (according to experimental data).

2. The probability of response (trace P) in i-th ISI was given by a simple equation (cf. Fig. 1B)

$$P = \begin{cases} 0 & \text{for } t < t_{ri} \\ 1 & \text{for } t \ge t_{ri} \end{cases}$$

The values of response time t_{ri} were computed according to the normal distribution with a mean t_r determined from (1) and standard deviation SD_r estimated from the curves $RI(t)$ (cf. Fig. 3).

3. The time sequence of the stimuli (trace Y) was determined as the train of impulses with the constant interstimulus intervals $\bar{y}$, corresponding to the stimulation rate R_y between 40 and 100 imp/s.

4. The response (trace Z) was generated simultaneously with the first stimulus which arrived at the time $t \ge t_r$.

5. After a response the background spike sequence was interrupted and the next spike of the background

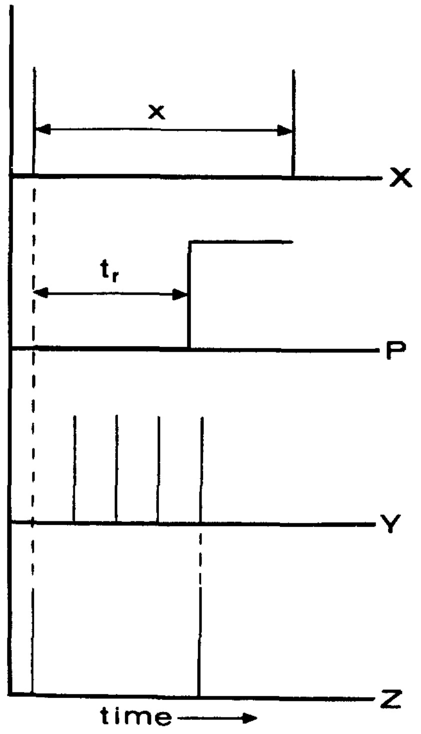

Fig. 6. Simulation principles: trace X – background spike train (x – ISI); trace P – response probability (t_r – corresponding response time); trace Y – stimulus train; trace Z – output spike train. Output spike is generated simultaneously with the first stimulus which arrives at the time $t \geq t_r$

sequence was generated in the appropriate interval with respect to the last output spike according to p. 1.

The sequence 2 to 5 was repeated until the total number of spikes in the background train was 300. After each simulation cycle, the mean background firing rate R_x was computed and then the parameters of the resulting output (response) train: mean ISI $\bar{z}$ and mean firing rate R_z, were determined from the computer simulation results. Finally, the excitability was computed in terms of the firing rate increment $\Delta R = R_z - R_x$.

3.2 Modelling results

The dependences $\Delta R(R_x)$ for the stimulation rate of 100 imp/s for all the five investigated motoneurones are shown in Fig. 7. The main features of these dependences are as follows:

1. As could be expected, for motoneurones with low t_{rs} values (# 1 and # 2), the firing rate increment was considerably higher than for the others (# 3, # 4, # 5).

2. On each curve two parts of different character could be distinguished corresponding to the two parts of the dependence $t_r(\bar{x})$.

3. In the lower firing rate range, ΔR for all the motoneurones decreased when the background firing rate increased.

4. In the range of higher firing rates, ΔR for motoneurones # 1, # 2, # 3 increased with increasing firing rate and for motoneurones # 4, # 5 it remained almost constant.

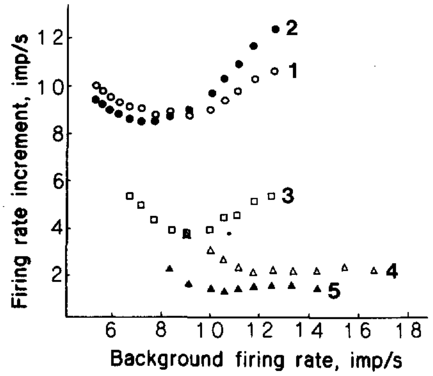

Fig. 7. Firing rate increment vs background firing rate for motoneurones # 1–5. Stimulation rate 100 imp/s

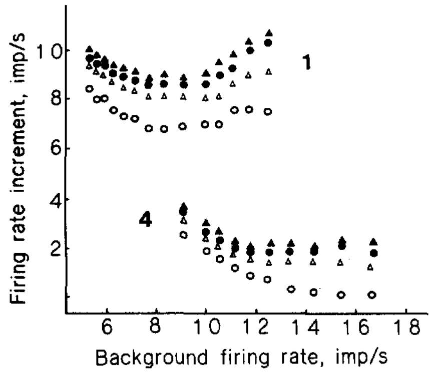

Fig. 8. Firing rate increment vs background firing rate for motoneurones # 1 and # 5. Stimulation rates: open circles – 40 imp/s; open triangles – 60 imp/s; heavy circles – 80 imp/s; heavy triangles – 100 imp/s

In Fig. 8 it can be seen that when the stimulation rate grew from 40 to 100 imp/s it did not produce a significant increase in stimulation efficiency especially for low background rates. For high background rates the firing rate increment increased by maximum 3 imp/s. It should be noted that output rates did not exceed the physiological range. Even when motoneurones with the lowest values of t_r were stimulated with 100 imp/s, the output rate was lower than 25 imp/s.

3.3 The relations between $t_r(\bar{x})$ and $\Delta R(R)$

In general terms, the influence of the parameters of the function $t_r(\bar{x})$ on the motoneuronal excitability to repetitive stimulation, $\Delta R(R_x)$, could be analysed provided the ISI variability and the stimulation rate were omitted. It is obvious that the output ISI would tend to converge to the value t_r if the stimulation rate increased. Therefore, the firing rate increment for a given $\bar{x}$ can be estimated roughly by its maximum value

$$\Delta R_m = 1/(t_r(\bar{x})) - 1/\bar{x} \tag{2}$$

This formula, in combination with (1), makes it possible to calculate the values of the function $\Delta R_m(R_x)$.

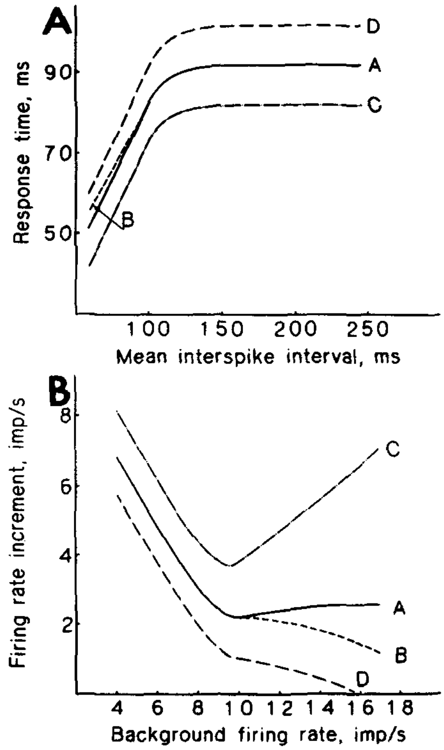

Fig. 9A,B. An illustration of the dependence between the functions $t_r(\bar{x})$ and $\Delta R(R_x)$. As a basis the experimental curve for the motoneurone # 5 was taken (*A*): **A** Hypothetical versions of $t_r(\bar{x})$ calculated according to (1). **B** Corresponding versions of $\Delta R_m(R_x)$ (2) marked with the same letters as in **A**

For this analysis, the approximation coefficients (form. 1) found for experimental function $t_r(\bar{x})$ regarding the motoneurone # 5 were employed (Fig. 9). $\Delta R_m(R_x)$ was calculated for the coefficients fitting the experimental data (*A*), for a changed slope, a, of the linear part (*B*), and for the case when whole curve $t_r(\bar{x})$ was moved up (*D*) and down (*C*) with respect to the t_r axis. When the curve was moved, the absolute values of ΔR_m changed, but the slope of the dependence $\Delta R_m(R_x)$ in the range of higher firing rates was also strongly affected. A very small increase in the slope, a, of $t_r(\bar{x})$ function changed the slope of $\Delta R_m(R_x)$ function from positive (*A*) to negative (*B*).

4 Discussion

From the analysis of experimental data (Kudina 1987, 1988; Miles et al. 1989, see also Fig. 2 of this paper), the typical dependence of the excitability to single stimuli on the background firing rate seems to be as follows: the excitability decreases when increasing the firing rate in the lower rate range and reaches a plateau in the higher rate range. The different curve for whole population of motoneurones in FCU obtained by Kudina and Churikova (1987) evidently resulted from averaging data collected for many motoneurones whose excitability functions were scattered widely over the plot (cf. Fig. 2).

The dependence of excitability to computer simulated repetitive stimulation on background firing rate in the range of lower firing rates for all the 5 investigated motoneurones, was the same as for single stimuli. In the higher rate range, these dependences were different for individual motoneurones. This may be explained by the existing differences in the approximation parameters of their functions $t_r(\bar{x})$ (cf. section 3.3). On the other hand, all these functions were similar in shape. An explanation of both similarity and differences is possible in terms of an interaction between the membrane potential trajectory of a firing motoneurone and the EPSP.

As it is clear from Fig. 1 and 5, the difference in the position of the curves $t_r(\bar{x})$ with respect to t_r axis may depend on the depth of a motoneurone interspike membrane potential trajectory as well as on an EPSP amplitude. The first one is directly dependent on the depth of AHP and may be different in different motoneurones. However, the conditions of our experiments restricted the sample of investigated motoneurones to the low-threshold part of the motoneuronal pool, so the differences in AHP depth could hardly be noticeable. We believe therefore that the main cause for differences in $t_r(\bar{x})$ functions of investigated motoneurones were inequalities in the EPSP amplitude. What also speaks in favour of this view is the experimentally established tendency towards certain correlation between the position of the curve $t_r(\bar{x})$ with respect to t_r axis and the slope of its linear part. The differences in EPSP amplitudes could well be expected in the experiments since the strength of the stimuli at the motoneuronal level could in no way be equalized in different experiments, and even in the same experiment, the *Ia* afferent inputs to different motoneurones could have had different strength.

If there had been two curves $t_r(\bar{x})$ of the same level, the slopes of their linear parts would have reflected the degree of divergence of the ramp phases of interspike potential trajectories at different firing rates. As it was shown, the values of t_r restrict from below the possible ISI length. Thus, the degree of ramp divergence should reflect the ability of a motoneurone to "resist" too big increase in firing rate due to additional excitatory input.

The excitability to repetitive stimulation (the dependence $\Delta R(R_x)$) in the higher rate range is influenced by the EPSP amplitude as well as by the intrinsic properties of a motoneurone revealing themselves as interspike membrane potential trajectory depth and ramp divergence at different firing rates. Various combinations of these factors as follows from Fig. 5 and 9, may result in obtaining various slopes of the dependence $\Delta R(R_x)$ in this range of background firing rates. This may explain various results obtained by Shapovalov (1972, 1975) for various motoneurones. Also functions $\Delta R(R_x)$ obtained by means of computer simulation for 5 real motoneurones had variety of slopes. However, the negative slopes as clear as in the case *B* or *D* in Fig. 9 were not found. This may be explained by the experimental tendency to correlation between the slopes of the linear parts of the functions $t_r(\bar{x})$ and their maximum values (Fig. 4B) since both correlated parameters have the contradictive influence on the function $\Delta R(R_x)$ (cf. Fig.

9). Computer simulation shows that this slope may depend also on the stimulation rate (see Fig. 8).

The difference in the results obtained for the same single motoneurones by applying stimulation with single stimuli as compared with repetitive stimulation also indicate that the indices used to estimate the excitability for each type of stimulation were not equivalent with each other. We suppose that the firing rate increment is a more natural measure of motoneuronal excitability, the same as the repetitive stimulation is closer to the physiological conditions than the stimulation with single stimuli.

Repetitive computer simulated stimulation in the present model was an analogue of the experimental stimulation of monosynaptic input which produced discrete EPSPs in the motoneurone. Both situations are rather artificial since under natural conditions a motoneurone is activated by distributed synaptic inflow from many converging sources. Nevertheless, Shapovalov (1972, 1975) has indicated possible physiological conditions when discrete monosynaptic EPSPs of low amplitude may influence motoneuronal discharges. He extensively investigated monosynaptic descending pathways from the cortex and brain stem to motoneurones and suggested that their function is to control motoneuronal firing rate by discrete EPSPs when motoneurone is already activated by other sources.

However, it is unknown to which extent the control mechanisms suggested by Shapovalov are functionally relevant. The computer simulated repetitive stimulation was therefore not intended to imitate any physiological process but rather to create quasi-experimental conditions for the investigation of factors which influence the motoneuronal excitability.

Acknowledgements. The authors are much indebted to Dr. L. Kudina for valuable advice and discussion and to Prof. R. B. Stein for helpful comments. This work was partially supported by the grant CBPR 11.9 (Dr. M. Piotrkiewicz).

References

Ashby P, Zilm D (1982a) Relationship between EPSP shape and crosscorrelation profile explored by computer simulation for studies on human motoneurones. Exp Brain Res 47:33–40

Ashby P, Zilm D (1982b) Characteristics of postsynaptic potentials produced in single human motoneurones by homonymous group 1 volleys. Exp Brain Res 47:41–48

Baldissera F, Gustafsson B (1974) Firing behaviour of a neurone model based on the afterhyperpolarization conductance time course and algebraical summation. Adaptation and steady state firing. Acta Physiol Scand 92:27–47

Eccles JC, Eccles RM, Lundberg A (1958) The action potentials of the alpha motoneurones supplying fast and slow muscles. J Physiol (London) 142:275–291

Fetz EE, Gustafsson B (1983) Relation between shapes of post-synaptic potentials and changes of firing probability of cat motoneurones. J Physiol (London) 341:387–410

Kostyukov AI, Ivanov YuN, Kryzhanovsky MV (1981) Probability of neuronal spike initiation as a curve-crossing problem for Gaussian stochastic processes. Biol Cybern 39:157–163

Kudina LP (1987) Excitability testing of human firing motoneurone during ISI. Neurophysiology (Kiev) 19:210–216 (in Russian)

Kudina LP (1988) Excitability of firing motoneurones tested by Ia afferent volleys in human triceps surae. Electroencephalogr Clin Neurophysiol 69:576–580

Kudina L, Churikova L (1987) Relationship between the discharge rate of a firing motoneurone and effectiveness of the excitatory Ia afferent volley in man. Neurophysiology (Kiev) 19:595–600 (in Russian)

Kudina LP, Churikova LI, Alexeeva NL (1989) Firing peculiarities of human motor units within the "subprimary range". Abstracts of the Sixth Intern Symp Motor Control '89, Albena 3–7 July

Khushivadze TH (1979) A comparison of motor unit activity in soleus and gastrocnemius muscles. Hum Physiol 5:102–109 (in Russian)

Matthews Peter BC (1984) Observation on the time course of the electromyographic response reflexly elicited by muscle vibration in man. J Physiol (London) 353:447–461

Miles TS, Türker KS, Nordström MA (1987) Reflex responses of motor units in human masseter muscle to electrical stimulation of the lip. Exp Brain Res 65:331–336

Miles TS, Türker KS, Le Th (1989) Ia reflexes and EPSPs in human soleus motorneurones. Exp Brain Res 77:628–636

Person RS, Kudina LP (1972) Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. Electroenceph Clin Neurophysiol 32:471–483

Shapovalov AI (1972) Extrapyramidal monosynaptic and disynaptic control of mammalian alpha-motoneurons. Brain Res 40:105–115

Shapovalov AI (1975) Neurones and synapses of supraspinal motor control systems. Nauka, Leningrad (In Russian)

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