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# NON-LINEAR SUMMATION OF UNIT SYNAPTIC POTENTIALS IN SPINAL MOTONEURONES OF THE CAT

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## SUMMARY

1. Monosynaptic excitatory post-synaptic potentials (EPSPs) produced in spinal motoneurones of the cat by stimulation of a single afferent fibre were recorded with intracellular electrodes.

2. In total, seventy-three triceps surae motoneurones were studied with stimulation of thirty-six different afferent fibres.

3. The mean amplitude of the EPSPs evoked by single afferent impulses ranged from 0·06 to 2·0 mV with an average of 0·27 mV.

4. The mean number of unit EPSPs responding to a single afferent impulse ($m$) was calculated from the number of failures. The values ranged from 0·7 to more than 5. About 10 % of the sample showed no failure of synaptic response in about 200 consecutive trials. The $m$ values for these synaptic responses were estimated to range from 5 to 15.

5. In the majority of tests, the observed amplitude fluctuations of monosynaptic EPSPs evoked by stimulation of a single fibre were less than those expected from Poisson's law. This discrepancy may be accounted for by non-linear summation of the unit EPSPs at dendritic synaptic sites.

6. It is suggested that the synaptic responses initiated at different sites of a motoneurone may summate linearly at the soma, although summation of unit EPSPs is non-linear at individual synaptic sites.

## INTRODUCTION

Monosynaptic excitatory post-synaptic potentials (EPSPs) produced in spinal motoneurones by stimulation of a single afferent fibre show a random fluctuation in amplitude with occasional failures of synaptic response (Katz & Miledi, 1963; Kuno, 1964; Burke, 1967; Letbetter, Willis & Thompson, 1968). A statistical analysis of the amplitude of such EPSPs has demonstrated that the synaptic response in the motoneurone is built

up of all-or-none unit potentials (unit EPSPs) which roughly correspond in amplitude to the spontaneously occurring miniature synaptic potentials (Katz & Miledi, 1963; Blankenship & Kuno, 1968).

In spinal motoneurones of the cat, the mean number of units responding to one impulse ($m$, mean quantum content) was estimated to be approximately unity so that the average amplitude of monosynaptic EPSPs evoked by single afferent impulses was usually close to that of spontaneous miniature potentials, i.e. 0·1–0·25 mV (Kuno, 1964; Blankenship & Kuno, 1968). In some instances, the calculated $m$ values were relatively high ($> 3$), but these were attributed to stimulation of more than one afferent fibre. In fact, when such large synaptic responses ($m > 3$) were tested, the amplitude fluctuations were significantly less than those expected from Poisson's law (Kuno, 1964). Thus, it was postulated that the deviation from the expected amplitude fluctuation at high values of $m$ is due to some interaction between the afferent terminals when several fibres are synchronously stimulated (Kuno, 1964; cf. also Martin & Veale, 1967).

On the other hand, Burke & Nelson (1966) found that impulses from certain afferent fibres can produce relatively large EPSPs in motoneurones (mean amplitudes of 0·7–1·6 mV) without failure of synaptic response. This observation raises the possibility that the $m$ values of monosynaptic EPSPs to single afferent impulses may vary widely from fibre to fibre. Therefore, the high values of $m$ occasionally observed by Kuno (1964) might have resulted from activity in single afferent fibres. A question then arises as to whether the discrepancy between the expected and observed EPSP amplitude fluctuations depends on the $m$ value rather than on the number of afferent fibres stimulated. With this surmise, the observed discrepancy would be due to some mechanism other than presynaptic interaction.

These problems provide the basis of the present study which evaluates in detail the $m$ of monosynaptic EPSPs to single afferent impulses in a large sample. The results will show that the $m$ values range from less than 1 to about 15 and that the deviation from the expected amplitude fluctuation may be accounted for by non-linear summation of the unit EPSPs at the dendritic synaptic sites. A preliminary report has been published elsewhere (Kuno & Miyahara, 1968).

## METHODS

The experiments were performed on adult cats anaesthetized with a single intraperitoneal injection of sodium pentobarbitone (Diabutal, Diamond Laboratories; 35 mg/kg). The spinal cord was cut at the first cervical level, and the brain was pithed. The animal was maintained by artificial respiration and immobilized by injections of gallamine triethiodide (Flaxedil, American Cyanamid Company). More than 8 hr always elapsed from initiation of anaesthesia to the time of the observations.

The experimental procedure was essentially similar to that described by Jack, Miller & Porter (1967) and Mendell & Henneman (1968). After lumbosacral laminectomy, the L 5 to S 2 dorsal roots on the left side were sectioned except for a small L 7 (or S1) filament. The afferent input to the spinal cord from the left hind limb was thus restricted to this small dorsal root filament from which the afferent impulses were monitored. In the left hind limb, the muscle nerve to the triceps surae was exposed, cut distally and divided into several bundles. After each division, the nerve bundle was stimulated, and the impulses were recorded from the intact dorsal root filament. The dissection was repeated until stimulation of the nerve bundle finally evoked activity of only one afferent fibre within the intact root filament. Evidence for the single fibre response was based on the all-or-none behaviour of the afferent impulse to a graded change in stimulus intensity from below threshold to twice threshold. Usually, three to seven of such bundles were prepared in each experiment. Other branches of the sciatic and femoral nerves were severed bilaterally. A few nerve branches supplying the glutei and small hip muscles were often left intact, and they caused some background discharges in the intact dorsal root filament (Figs. 1 and 4). All exposed nervous tissues were covered with pools of mineral oil, and external heat aided in keeping the body temperature between 34·5 and 37·5° C.

Intracellular recording from spinal motoneurones was made with glass micro-electrodes filled with 2 M potassium citrate solution. Since the ventral roots were intact, recording from triceps surae motoneurones could be identified by antidromic action potentials induced by stimulation of the muscle nerve. Once the motoneurone was impaled with a stable resting potential, each of the triceps surae nerve bundle containing one afferent fibre connexion to the cord was stimulated at 1/sec. Monosynaptic EPSPs evoked in the motoneurone by stimulation of the nerve bundle were identified by the short latency (less than 1 msec) between the synaptic response and the afferent impulse simultaneously recorded from the intact dorsal root filament (see Figs. 1 and 4). Before and after a series of observations on the monosynaptic EPSPs, action potentials of the motoneurone were monitored, and those units with spikes of less than 50 mV were discarded.

## RESULTS

*m values of EPSPs to single afferent impulses.* Figure 1 illustrates a series of monosynaptic EPSPs recorded from two different motoneurones (*A* and *B*) following stimulation of single afferent fibres. The latency of the EPSPs (upper traces, arrows) measured from the afferent impulses recorded from the dorsal root filament (lower traces, dotted lines) showed a slight fluctuation within 0·3 msec. In agreement with previous observations (Katz & Miledi, 1963; Kuno, 1964; Burke, 1967; Letbetter *et al.* 1968), the same afferent impulse evoked monosynaptic EPSPs of varying amplitudes, and some impulses failed to produce any detectable synaptic responses (Fig. 1*A*). However, in a few cases (about 10 %) single afferent impulses produced relatively large EPSPs, and in these instances no failure of synaptic response was recognized in about 200 consecutive trials (Fig. 1*B*).

The mean amplitudes of monosynaptic EPSPs to single afferent impulses were measured in eighty-three different tests; these included observations obtained by stimulation of one afferent fibre diverging to different motoneurones and by stimulation of different afferent fibres converging upon the same motoneurone. A total of seventy-three triceps surae moto-

neurones were studied with stimulation of thirty-six different afferent fibres arising from the triceps surae muscle. Figure 2*A* shows the frequency distribution of the mean amplitudes of EPSPs. They varied from 0·06 to 2·0 mV with the average of 0·27 mV. This exceeded the range of the previous estimate of 0·1–0·25 mV (Kuno, 1964) and was comparable

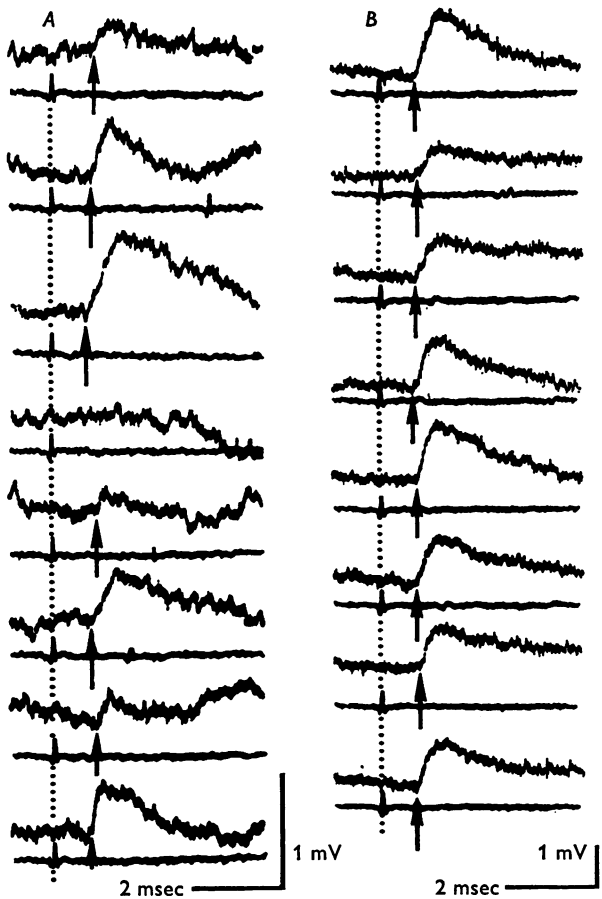


Fig. 1. Monosynaptic EPSPs (upper traces) recorded from two different triceps surae motoneurones (*A* and *B*) following stimulation of single afferent fibres from the triceps surae muscle at 1/sec. Lower traces, afferent impulses (dotted lines) simultaneously recorded from an intact dorsal root filament. Arrows indicate the onset of EPSPs (upper traces). $m_i = 3{\cdot}0$ in *A*. The EPSPs in *B* showed no failure with 204 trials.

to the values reported by Mendell & Henneman (1968; 0·20–0·70 mV) and by Burke (1967; 0·16–0·96 mV). However, the mean amplitudes of EPSPs for the majority (60 %) of the sample were still between 0·1 and 0·2 mV (Fig. 2*A*).

From the statistical assumptions on which the Poisson analysis is based (Del Castillo & Katz, 1954), the mean number of unit EPSPs following one afferent impulse ($m$, mean quantum content) may be given by

$$m = \log_e \frac{\text{number of afferent impulses applied}}{\text{number of failures of synaptic responses}}.$$

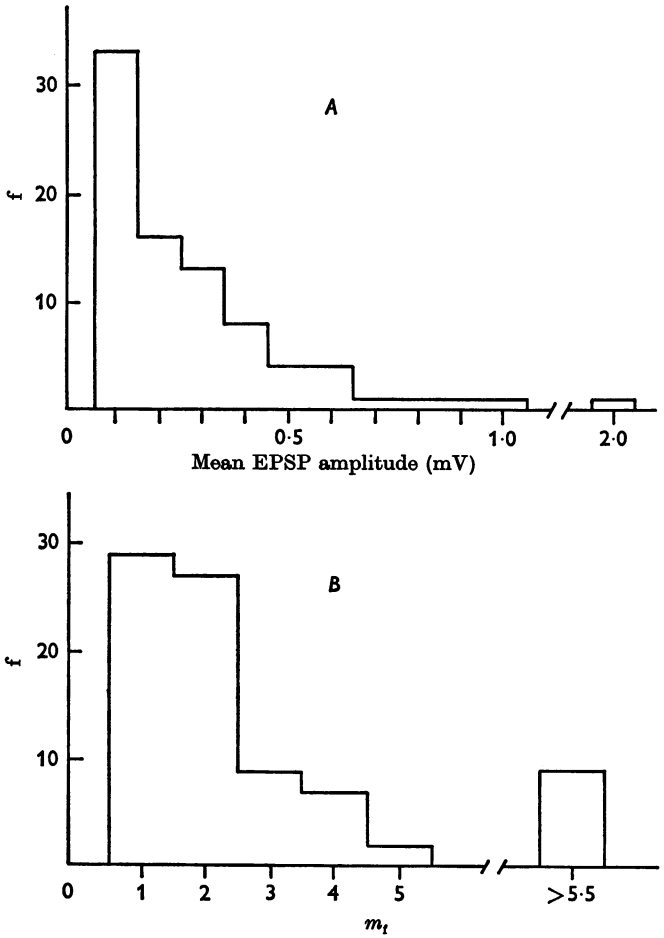


Fig. 2. Frequency distributions of mean EPSP amplitudes ($A$) and $m_t$ values ($B$) of eighty-three different synapses tested with stimulation of single afferent fibres. $m_t$, $m$ values calculated from the number of failures of synaptic response. Ordinates, the number of observations.

Figure 2$B$ shows the distribution of the $m$ values calculated for the eighty-three tests. The values ranged from less than 1 (0·7) to about 5 (5·4) in the majority of tests. Although $m$ values were about one in 35 % of the sample, the average $m$ was between 2 and 3. This contrasts with the previous sug-

gestion that the $m$ of monosynaptic EPSPs to single afferent impulses is approximately unity and does not vary widely from fibre to fibre (Kuno, 1964). In addition, about 10 % of the sample showed no failure of synaptic response for about 200 trials (Fig. 1*B*). These results were grouped in a class of $m > 5{\cdot}5$ in Fig. 2*B*, since the $m$ values could not be estimated from the above relationship (however, see below). Burke & Nelson (1966) also found that impulses from some afferent fibres activated by muscle stretch produce large EPSPs in motoneurones without failures (also, see Katz & Miledi, 1963).

*m values and amplitude fluctuations of EPSPs.* If the synaptic response in a motoneurone is built up of unit potentials whose chance of occurrence to an afferent impulse may be described by Poisson's law, the value of $m$ should also be given by

$$m = \frac{1}{(\mathrm{CV})^2},$$

where CV is the coefficient of variation of the amplitude distribution of observed EPSPs (del Castillo & Katz, 1954). Figure 3 shows the relationship between the $m$ values calculated from the coefficient of variation ($m_{\mathrm{CV}}$) and those obtained from the number of failures of synaptic response ($m_f$) for the eighty-three different tests (open circles and arrows). Although the values obtained by these two independent measurements were approximately equal at low level of $m_f$, those EPSPs with $m_f > 3$ showed a considerable discrepancy between $m_{\mathrm{CV}}$ and $m_f$ (Fig. 3). This tendency was essentially similar to that previously ascribed to interaction between the presynaptic terminals when a large number of afferent fibres were synchronously stimulated (Kuno, 1964). However, this interpretation now seems unjustified, since the discrepancy still exists in the present tests in which afferent stimulation is limited to a single fibre. Thus, the discrepancy between the observed and expected EPSP amplitude fluctuations must be dependent on the $m$ value but not on the number of afferent fibres stimulated.

*Non-linear summation of unit EPSPs.* A similar discrepancy between the observed and expected amplitude fluctuations at high values of $m$ has been noted in the neuromuscular junction (del Castillo & Katz, 1954) and could be accounted for by non-linear summation of the unit potentials making up the end-plate potential (Martin, 1955). At first sight, such non-linear summation appears unlikely to occur in spinal motoneurones since the amplitude of the unit EPSPs is 0·1–0·25 mV (Kuno, 1964), so that the synaptic response with $m = 3$ is still very small compared to the driving potential for the EPSP (the EPSP equilibrium potential minus the resting potential). However, it has recently been suggested that the distribution

of most of the synapses formed by afferent terminals is restricted to the dendrites in mammalian motoneurones (Bodian, 1966; Terzuolo & Llinás, 1966; Rall, Burke, Smith, Nelson & Frank, 1967; however, cf. Illis, 1964). Since the input resistance of dendrites must be higher than that of the soma (Katz, 1966, pp. 151–152), the unit EPSPs at the dendritic synaptic sites may be considerably greater than those observed in the soma (Katz & Thesleff, 1957). Under this condition, it is possible that summation of a few unit EPSPs at synaptic sites congregating on a dendrite (see below)

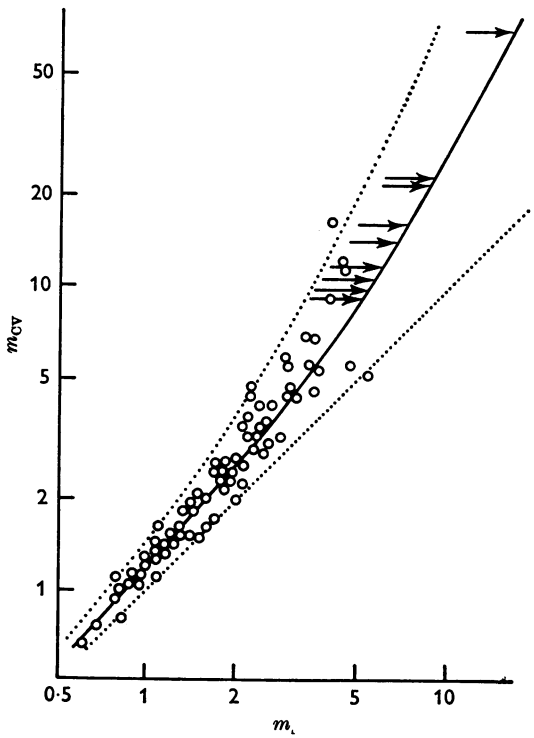


Fig. 3. Relation between $m$ values estimated from the coefficient of variation ($m_{CV}$) and those calculated from the number of failures ($m_t$). Solid curve, the theoretical relation. Dotted line and curve, limits of scatter for the observed points. Arrows indicate the $m_{CV}$ values for those EPSPs with no failure. For theoretical basis of the curves, see text.

can significantly reduce the driving potential for the EPSP so that the increment of the EPSP amplitude by additional units would no longer be linear (del Castillo & Katz, 1954; Martin, 1955). Consequently, the range of variation of EPSP amplitudes would be smaller than that expected from Poisson's law.

This assumption may be tested by applying the method used for analysis

of non-linear summation in the neuromuscular junction. From the above notion, the $m_{CV}$ value would be greater than the $m_f$, and this relation is given by the formula (Martin, 1965)

$$m_{CV} = m_f \left(1 - \frac{\bar{v}}{V_0}\right)^{-2} \tag{1}$$

where $\bar{v}$ is the average EPSP amplitude at the synaptic site and $V_0$ is the driving potential for the EPSP. With allowance for non-linear summation of the unit potentials (Martin, 1955)

$$\bar{v} = \frac{m_f v_1 V_0}{m_f v_1 + V_0}, \tag{2}$$

where $v_1$ is the average amplitude of the unit EPSPs at the synaptic site. Therefore, from (1) and (2),

$$m_{CV} = m_f(1 + k m_f)^2 \tag{3}$$

where $k = v_1/V_0$. As shown in Fig. 3, the observed relationship (open circles) was in good agreement with the theoretical prediction (continuous line) at $k = 0{\cdot}07$.

The degree of non-linear summation ($km_f$) depends on the amplitude of unit EPSPs ($v_1$), and hence on the post-synaptic input resistance at the synaptic site (Katz & Thesleff, 1957), as well as on the $m_f$ value. The input resistance of the motoneurone must be the lowest at the soma and increases with distance from the soma because of the taper of dendrites. This implies that non-linear summation of unit EPSPs becomes progressively less as the synaptic site approaches to the soma since the unit EPSP size at the soma would be negligible compared with the driving potential for the EPSP. Therefore, the relation between $m_{CV}$ and $m_f$ should have a lower limit at $k \doteqdot 0$, and hence $m_{CV} = m_f$. This is indicated by the lower dotted line in Fig. 3 which agrees well with the limit of scatter for the observed points. The observed relation between $m_{CV}$ and $m_f$ also showed an approximate upper limit at $k = 0{\cdot}2$ (upper dotted curve in Fig. 3). Since the driving potential for the EPSP ($V_0$) is 70 mV (Coombs, Eccles & Fatt, 1955), the mean amplitude of unit EPSPs at the dendritic synaptic site ($v_1$) would be, at most, about 15 mV ($k = 0{\cdot}2$) and is approximately 5 mV on the average ($k = 0{\cdot}07$).

From the above, it is also possible to estimate the $m_f$ values for those EPSPs which showed no failure in about 200 trials. The arrows in Fig. 3 indicate the $m$ values calculated from the coefficient of variation ($m_{CV}$) for these synaptic responses. The corresponding $m_f$ values were in a range of 5–15 (cf. Burke & Nelson, 1966).

*Summation of EPSPs from two different inputs.* In Fig. 3, those points

lying on the line with $m_{CV} = m_t$ were only 10 % of the sample. This suggests that the majority of afferent terminals make synaptic contacts on the dendrites some distance from the soma. This situation provides another test of the present assumption.

When synaptic responses are elicited at two different dendrites of a motoneurone, the EPSPs would spread electrotonically to the soma. Therefore, although the unit EPSPs may summate non-linearly at each synaptic site, the synaptic potentials from the two inputs should summate linearly

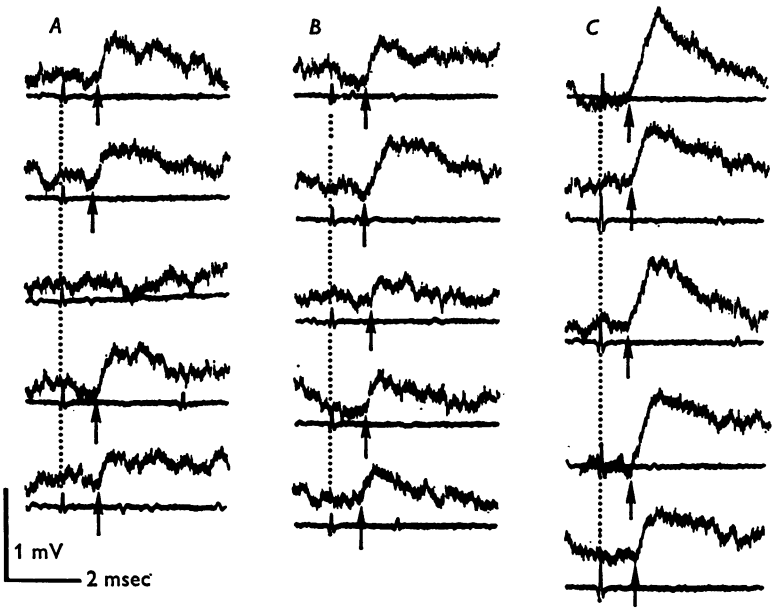


Fig. 4. Monosynaptic EPSPs recorded from a medial gastrocnemius motoneurone. *A*, following stimulation of a single afferent fibre from the medial gastrocnemius muscle ($m_t = 1{\cdot}4$). *B*, following stimulation of a single afferent fibre from the lateral gastrocnemius muscle ($m_t = 2{\cdot}4$). *C* following simultaneous stimulation of these two afferent fibres ('$m_t$' = 4·8). Upper traces, EPSPs, the onset of which is pointed by arrows. Lower traces, afferent impulses (dotted line) recorded from an intact dorsal root filament. The results are graphically shown by squares in Fig. 5.

at the soma. Consequently, the synaptic responses evoked by simultaneous activation of two afferent fibres might be expected to show less non-linear summation than those obtained by stimulation of a single fibre.

Figure 4*A* shows monosynaptic EPSPs produced in a medial gastrocnemius motoneurone by stimulation of a single afferent fibre from the medial gastrocnemius muscle. Monosynaptic EPSPs were also recorded from the same motoneurone following stimulation of a single afferent fibre from the lateral gastrocnemius muscle (Fig. 4*B*). The mean amplitude

of the monosynaptic EPSPs was clearly increased by simultaneous stimulation of these two afferent fibres (Fig. 4*C*). The '$m_f$' values obtained by stimulation of two fibres approximately agreed (within 30%) with the algebraic sum of the $m_f$ values observed by separate stimulation of each fibre (in four experiments). This further indicates the absence of presynaptic interaction between different afferent fibres.

Figure 5 shows the relation between $m_f$ and $m_{CV}$ for these synaptic responses. As previously shown (Fig. 3), the $m_{CV}$ was invariably greater than the $m_f$. However, the synaptic responses evoked by simultaneous

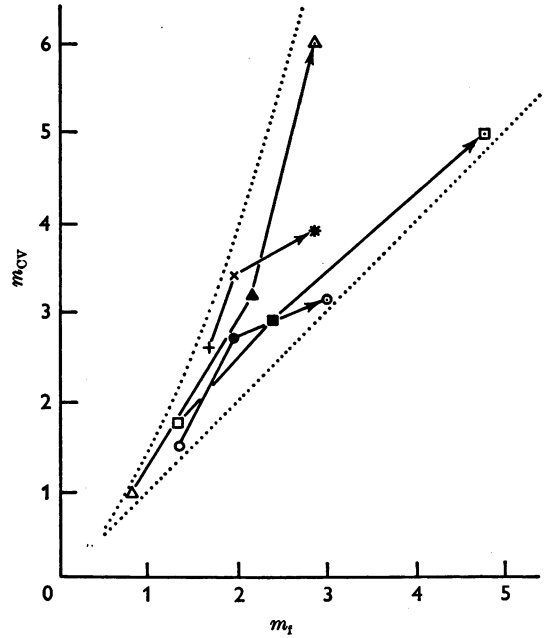


Fig. 5. Relation between $m$ values estimated from the coefficient of variation ($m_{CV}$) and those calculated from the number of failures ($m_f$). Dotted line and curve, limits of the relationship obtained from Fig. 3. Results from four different motoneurones. In each experiment, EPSPs were recorded following stimulation of a single fibre (○, △, □, +), another afferent fibre (●, ▲, ■, ×) and simultaneous stimulation of the two afferent fibres (⊙, ◬, ⊡, *). Squares were obtained from the experiment shown in Fig. 4.

stimulation of two afferent fibres showed a smaller difference between the '$m_{CV}$' and the '$m_f$' in spite of an increase in the '$m_f$'. For example, impulses from one afferent fibre alone produced monosynaptic EPSPs with $m_f = 1{\cdot}4$ and $m_{CV} = 1{\cdot}5$ (open circle in Fig. 5). The $m_f$ and $m_{CV}$ of the synaptic responses evoked in the same motoneurone by impulses in another afferent fibre were 2·0 and 2·7 respectively (filled circle). However, the

'$m_f$' (3·0) and '$m_{CV}$' (3·1) values were almost identical in the synaptic responses elicited by simultaneous stimulation of these two fibres (double circle pointed by arrow). Three other experiments showed essentially the same tendency, except one (triangles) in which the synaptic responses evoked by stimulation of two fibres (double triangle pointed by arrow) gave a larger difference between the '$m_f$' and the '$m_{CV}$' than for stimulation of a single fibre (open and filled triangles). The explanation for the results of this particular experiment remains uncertain, although this could occur if the two synaptic sites were closely located on the same dendrite. In general, however, the results suggest that the synaptic responses initiated at different sites of a motoneurone tend to summate linearly in the soma, while summation of the unit EPSPs is non-linear at individual synaptic sites.

## DISCUSSION

In agreement with Burke & Nelson (1966; also, cf. Katz & Miledi, 1963), about 10 % of the present sample showed no failure of synaptic response when approximately 200 stimuli were applied to a single afferent fibre. The $m$ values of these large EPSPs were estimated to be in a range of 5–15. However, it should be noted that the $m$ values of about 35 % of the sample were approximately unity (Fig. 2*B*). Mendell & Henneman (1968) could detect synaptic responses with the mean amplitude of 0·017 mV by the use of an averaging computer. In contrast, the smallest mean amplitude of EPSPs observed in the present study was 0·06 mV. It was possible that some small monosynaptic EPSPs were overlooked in the present test, so that the lower limit of the $m$ value was uncertain. However, it appears reasonable to conclude that the $m$ values of monosynaptic EPSPs to single afferent impulses vary from less than 1 to about 15 with the average between 2 and 3.

It has previously been shown that the discrepancy between the observed and expected EPSP amplitude fluctuations cannot be explained on the basis of a binomial distribution (Kuno, 1964). Similarly, the assumption of presynaptic interaction was also excluded (see Results). The present study indicates that the discrepancy may be explained adequately by assuming non-linear summation of the unit EPSPs at synaptic sites remote from the recording point. This behaviour is basically similar to that of the unit potentials making up the end-plate potential in the neuromuscular junction (Martin, 1955). However, non-linear summation of the unit EPSPs in the motoneurone depends on the synaptic location as well as the $m$ value. Thus, synaptic responses initiated at the soma would show practically linear summation, since the amplitude of the unit EPSPs at the soma would be negligible compared with the driving potential for the EPSP.

The mean amplitude of the unit EPSPs evoked at the soma may be calculated from those EPSPs with $m_f \doteqdot m_{CV}$ (points lying on the lower dotted line in Fig. 3). The average value was 0·10 mV with a range of 0·06–0·16 mV (Kuno & Miyahara, 1969). Since the average input resistance of these motoneurones was approximately 0·8 MΩ, the shunting resistance by a unit EPSP may be estimated as about 600 MΩ (or equivalent to $17 \times 10^{-10}$ mhos) which is comparable to a previous estimate (Kuno, 1964) and to that obtained in the avian ciliary ganglion (Martin & Pilar, 1964).

However, the majority of afferent terminals (about 90%) appear to make synaptic contacts on the dendrites where the input resistance is higher than in the soma. The amplitude of the unit EPSPs at the dendritic synaptic sites calculated from the $m_{CV}$–$m_f$ relation was approximately 5 mV on the average. If one assumes that the increment of conductance produced by the unit amount of transmitter is constant ($17 \times 10^{-10}$ mhos), the results imply that the input resistance at the dendritic synaptic sites is about 40–50 MΩ on the average.

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