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ANALYSIS OF SYNAPTIC EFFICACY IN SPINAL MOTONEURONES FROM 'QUANTUM' ASPECTS

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SUMMARY

1. Synaptic responses of triceps surae motoneurones of the cat following stimulation of single afferent fibres were examined by intracellular recording techniques.

2. The mean quantum content (m) of monosynaptic excitatory postsynaptic potentials (EPSPs) was independent of the type of motoneurone recorded and of the afferent fibre stimulated. There was no significant difference in m value between homonymous and heteronymous synapses.

3. A positive correlation was found between the amplitude of unit EPSPs and the input resistance of motoneurones. The difference in the amplitude of unit EPSPs appears to be responsible for the higher synaptic efficacy in slow-conducting motoneurones than in fast-conducting motoneurones.

4. There was no significant difference in the time course of monosynaptic EPSPs evoked by impulses from homonymous and heteronymous afferent fibres.

5. The ratio of monosynaptic connexions from a given afferent fibre was significantly greater on to homonymous than to heteronymous motoneurones. It is concluded that the difference in efficacy between homonymous and heteronymous synaptic transmission is due to the difference in the number of afferent fibres converging upon these motoneurones.

INTRODUCTION

The quantum hypothesis of synaptic transmission originally proposed by del Castillo & Katz (1954) for the neuromuscular junction has been shown to be applicable to the synaptic action on spinal motoneurones (Katz & Miledi, 1963; Kuno, 1964*a*, *b*; Burke, 1967*a*; Blankenship & Kuno, 1968; Kuno & Miyahara, 1969). Thus, the monosynaptic excitatory postsynaptic potential (EPSP) evoked in a spinal motoneurone by impulses in

a single afferent fibre is composed of all-or-none unit potentials (unit EPSPs), each with a certain probability of response to a nerve impulse. Under this condition, the average amplitude of monosynaptic EPSPs is determined by the average amplitude of unit EPSPs (v_1) and the mean number of units responding to one impulse (m, mean quantum content). Therefore, if one defines 'synaptic efficacy' in terms of the EPSP amplitude in response to a certain afferent input, synaptic efficacy (E) will be given, at first approximation, by $E = N.m.v_1$, where N is the number of afferent fibres converging on to the motoneurone.

Synaptic efficacy to a given afferent input depends on the afferent source as well as on the type of motoneurone. For example, it has been shown (Eccles, Eccles & Lundberg, 1957; Burke, 1968; also, see Lloyd, 1946) that an afferent volley from a skeletal muscle produces larger monosynaptic EPSPs in the motoneurone which innervates the muscle (homonymous) than in motoneurones subserving the synergists (heteronymous). Similarly, synaptic efficacy is higher in 'tonic' motoneurones with relatively slow axonal conduction velocities than in 'phasic' motoneurones with fast conduction velocities (Denny-Brown, 1929; Granit, Henatsch & Steg, 1956; Eccles *et al.* 1957; Kuno, 1959; Henneman, Somjen & Carpenter, 1965; Burke, 1968).

A previous study (Kuno & Miyahara, 1969) has shown that the m values vary from less than 1 to about 15 in different tests on spinal motoneurones. The amplitude of unit EPSPs (v_1) also varies from motoneurone to motoneurone, ranging from about 0·1 mV (Kuno, 1964*a*) to 0·7 mV (Burke, 1967*a*). The question may then arise as to whether the high values of m and v_1 are restricted only to those synapses formed by a certain type of afferent fibres and/or motoneurones specialized to give high synaptic efficacy. Alternatively, synaptic efficacy could be determined simply by the number of afferent fibres (N) converging on to a certain group of motoneurones. The present study aims to answer these questions. Preliminary results have been published elsewhere (Kuno & Miyahara, 1968*b*).

METHODS

The results to be presented in this paper were largely obtained from experiments reported previously (Kuno & Miyahara, 1969). Adult cats were anaesthetized by a single intraperitoneal injection of sodium pentobarbitone (Diabutal, Diamond Laboratories; 35 mg/kg). The spinal cord was severed at the first cervical level, and the brain was destroyed. The animal was maintained by artificial respiration and immobilized by injections of gallamine triethiodide (Flaxedil, American Cyanamid Company). After a lumbosacral laminectomy, all the dorsal roots from L5 to S2 on the left side were cut except for a small filament separated from the L7 or S1 dorsal root. This filament was prepared for the recording of afferent impulses initiated by electrical stimulation of the left triceps surae muscle nerve. The triceps surae (TS) nerve was cut distally and divided into medial gastrocnemius (MG)

and lateral gastrocnemius plus soleus (LGS) branches. These nerve branches were further dissected into several bundles such that stimulation of each nerve bundle activated only one afferent fibre in the intact dorsal root filament. The single fibre response was evidenced by the all-or-none behaviour of the afferent impulse to graded changes in stimulus intensity.

Intracellular recording from lumbosacral motoneurones was performed with glass microelectrodes filled with 2 M potassium citrate solution. Since the ventral roots were intact, the triceps surae motoneurones could be identified as MG or LGS motoneurones by the antidromic action potential induced by stimulation of the corresponding muscle nerve branch. Monosynaptic EPSPs evoked in the motoneurone by stimulation of nerve bundles were identified by the short latency (less than 1 msec) measured from the afferent impulses recorded from the intact dorsal root filament. In a few experiments, the EPSPs were led to a signal-averaging computer (Enhancetron 1024, Nuclear Data, Inc.) for clearer extraction of the responses from the background noise (see Fig. 7).

RESULTS

m values of EPSPs in different synapses. Monosynaptic EPSPs evoked 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*a*, *b*; Burke, 1967*a*; Letbetter, Willis & Thomson, 1968; Kuno & Miyahara, 1969). The m values calculated from the number of failures and from the coefficient of variation of the EPSP amplitudes ranged from less than 1 to about 15 (Kuno & Miyahara, 1969). Figure 1 illustrates monosynaptic EPSPs produced in two different motoneurones (*A* and *B*) by stimulation of the same afferent fibre. In one motoneurone (*A*), the afferent impulses evoked relatively small EPSPs, and the calculated m value was about 2·1. Impulses in the same afferent fibre showed only one failure of synaptic response for over 200 trials in another motoneurone (*B*), and m was 5·4. The mean amplitudes of the EPSPs were 0·18 mV in the former motoneurone (*A*) and 0·54 mV in the latter (*B*).

Figure 2 shows the relation between m values of monosynaptic EPSPs and the conduction velocity of fibres which were used for afferent stimulation. The results include the m values of EPSPs evoked by stimulation of the same afferent fibre diverging to different motoneurones (Fig. 1) as well as those obtained by stimulation of different fibres converging on to the same motoneurone (Fig. 3). In about 10% of the sample, there was no failure of synaptic response for about 200 consecutive impulses applied to a single afferent fibre (Burke & Nelson, 1966; Kuno & Miyahara, 1969). Since the m values of these EPSPs are obviously larger than 5·5, they are shown as circles with arrows in Fig. 2. The scatter of m values over the whole spectrum of afferent fibres tested suggests that there is no specific group of afferent fibres with high or low synaptic efficacy on spinal motoneurones.

One may surmise that a certain group of motoneurones might receive synaptic connexions from afferent fibres with high values of m. To test this

possibility, monosynaptic EPSPs were evoked in the same motoneurone by stimulation of two different afferent fibres (Fig. 3*A* and *B*). The *m* value of the EPSPs elicited by stimulation of one afferent fibre (*A*) was about 2·2, while impulses from another fibre (*B*) showed no failure of synaptic response in about 200 trials. In a number of tests, the *m* values as well as the mean amplitudes of EPSPs evoked in the same motoneurone by impulses from different afferent fibres varied in a manner similar to those produced by stimulation of the same fibre diverging on to different motoneurones

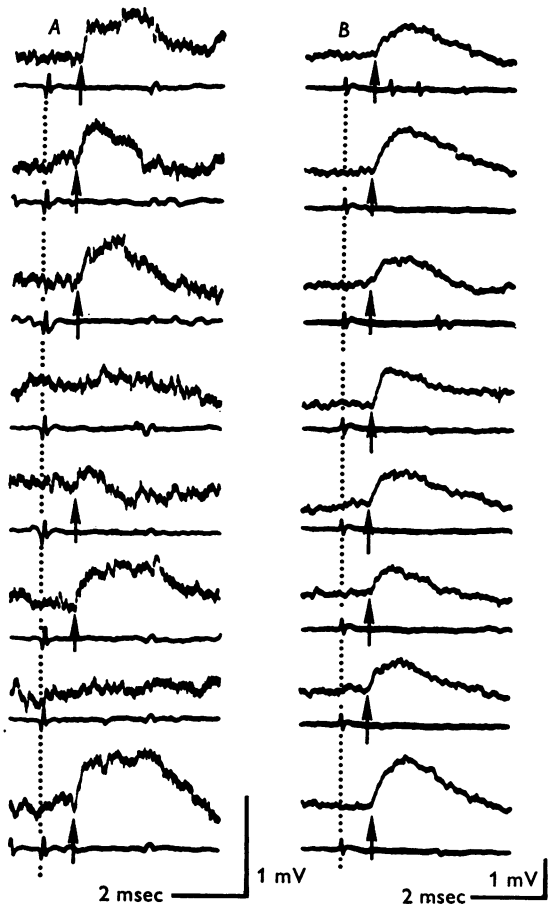

Fig. 1. Monosynaptic EPSPs produced in two different medial gastrocnemius motoneurones (*A* and *B*) by stimulation of one afferent fibre. Lower traces, afferent impulses recorded from a dorsal root filament (dotted lines). Upper traces, EPSPs with arrows showing the onset. Average amplitudes of the EPSPs were 0·18 mV for *A* and 0·54 mV for *B*. *m* values, 2·1 and 5·4 for *A* and *B* respectively. Note, the difference in shape of afferent impulses between *A* and *B* is due to application of saline solution to the dorsal root filament.

(cf. Figs. 1 and 3). In addition, there was no correlation between the m values and the axonal conduction velocity of motoneurones from which the EPSPs were recorded (Fig. 4). The m value also failed to show any correlation with the input resistance of motoneurones. Thus, there is no particular group of motoneurones which receive synapses with high values of m. Therefore, the difference in synaptic efficacy between fast- and slow

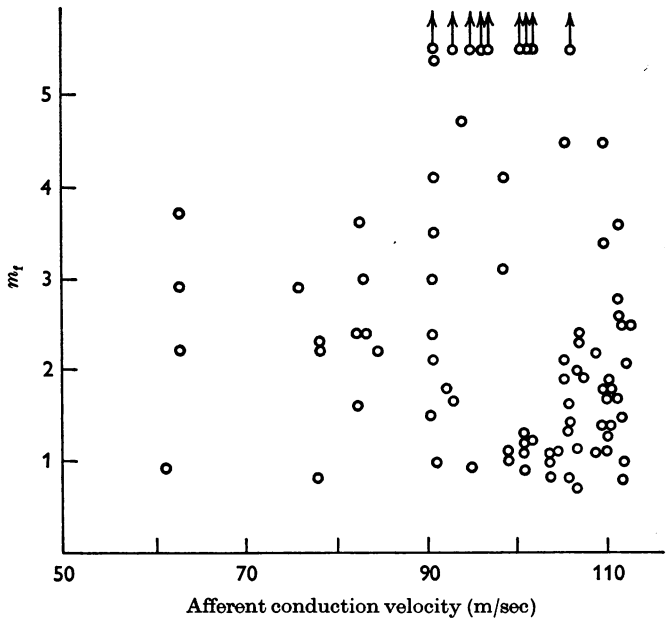

Fig. 2. Relation between m calculated from the number of failures of synaptic response and the conduction velocity of the afferent fibres stimulated. Open circles with arrows indicate the EPSPs which showed no failure in about 200 consecutive trials.

conducting motoneurones cannot be attributed to the variation in m values.

Figure 5 shows the distribution of m values for monosynaptic EPSPs obtained from sixty-four medial gastrocnemius motoneurones. The upper sample includes only those synaptic responses evoked by stimulation of single afferent fibres arising from the medial gastrocnemius muscle (homonymous), while the lower distribution is for the EPSPs produced by afferent impulses from the lateral gastrocnemius plus soleus muscles (heteronymous). There was no significant difference in the average as well as in the range of m values between homonymous and heteronymous synapses.

Amplitude of unit EPSP in different motoneurones. The amplitude of the

unit potentials (v_1) making up the EPSP may be calculated from the relation (del Castillo & Katz, 1954),

$$v_1 = \frac{\text{mean EPSP amplitude}}{\text{mean quantum content } (m)}.$$

However, if the presynaptic terminals are located on remote dendrites, there would be non-linear summation of the unit EPSPs at these synaptic sites (Kuno & Miyahara, 1969). Consequently, the amplitude fluctuation of

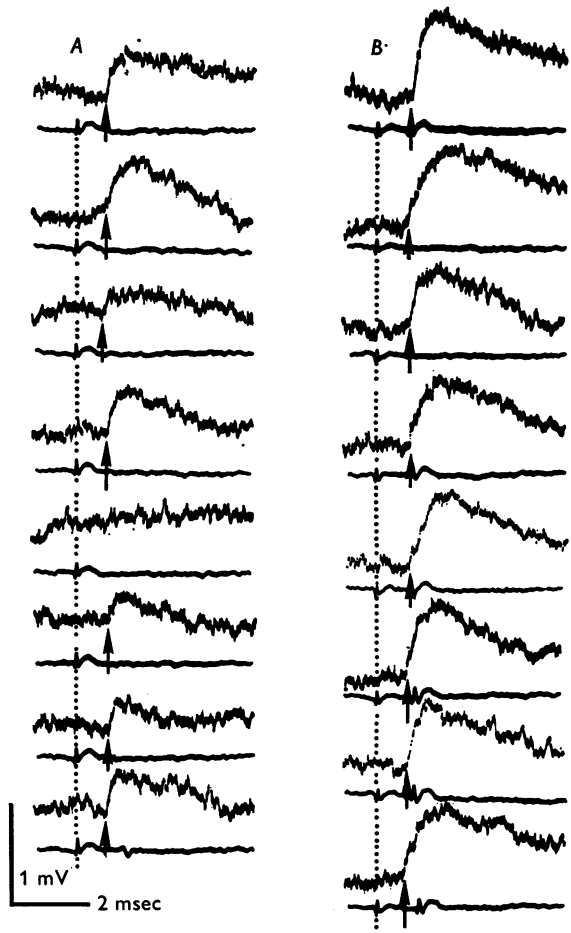

Fig. 3. Monosynaptic EPSPs recorded from the same motoneurone but with stimulation of two different afferent fibres (*A* and *B*). The arrows indicate the onset of the EPSPs (upper traces). Afferent impulses recorded from a dorsal root filament are shown by dotted lines (lower traces). Average amplitudes of the EPSPs were 0·27 mV for *A* and 0·66 mV for *B*. *m* was 2·2 for *A*. No failure occurred in *B* with 211 trials. *m* calculated from the coefficient of variation for *B* was 9·7.

the EPSPs would be less than that expected from Poisson's distribution, and the above relation for these synaptic responses would lead to an underestimation of v_1. The v_1 was, therefore, calculated only from those EPSPs in which m values obtained from the number of failures (m_f) deviated less than 30% from m values estimated from the coefficient of variation (m_{CV}).

Figure 6*A* shows the relation between the v_1 and the axonal conduction velocity of motoneurones from which the EPSPs were recorded. The line

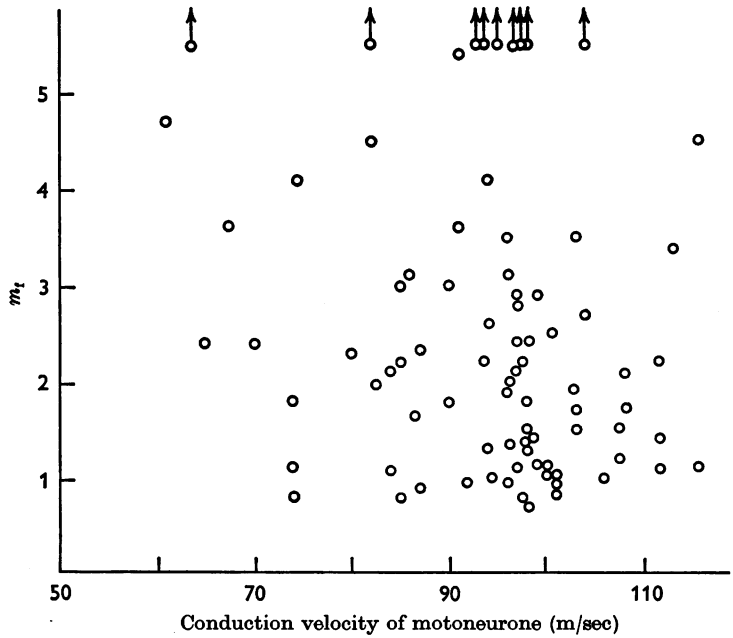

Fig. 4. Relation between m calculated from the number of failures of synaptic response and the axonal conduction velocity of motoneurones tested. Open circles with arrows indicate the EPSPs which showed no failure in about 200 trials.

best fitting the points was drawn by the method of least squares. Although there was a tendency for the slow-conducting motoneurones to possess larger unit EPSPs than fast-conducting motoneurones, the slope of the negative regression line was not statistically different from zero.

In spinal motoneurones of the cat, Kernall (1966) and Burke (1967*b*) found that the input resistance of motoneurones is inversely related to the axonal conduction velocity. By analogy with the neuromuscular junction (Katz & Thesleff, 1957), it has been suggested that the amplitude of unit EPSPs may depend on the input resistance of motoneurones (Kuno, 1964*a*; Henneman *et al.* 1965; Blankenship & Kuno, 1968; Burke, 1968; Kuno & Miyahara, 1969). This relation is clearly shown in Figure 6*B*. The input

resistance of motoneurones was measured either by changes in the membrane potential or by changes of the antidromic spike height during the passage of depolarizing and hyperpolarizing current pulses across the motoneurone membrane (Frank & Fuortes, 1956). The relation between the input resistance and v_1 was linear with a regression coefficient of 0·74

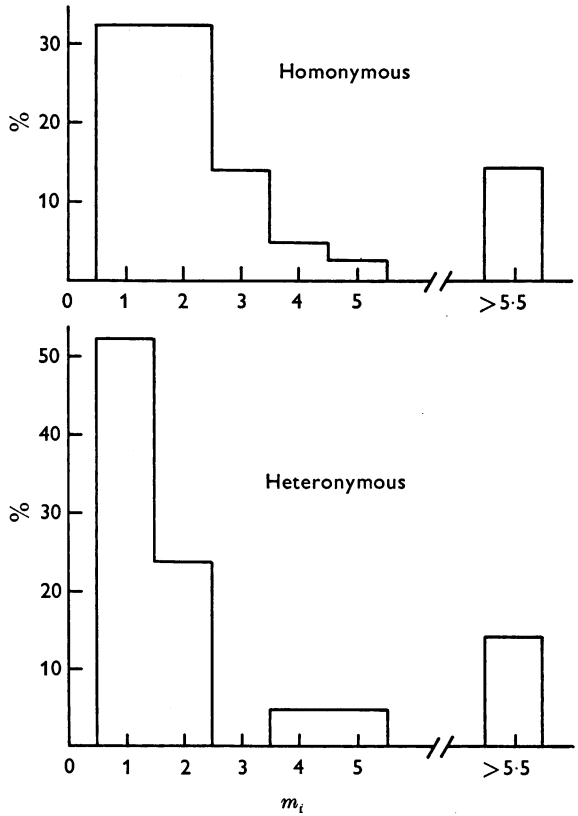

Fig. 5. Histograms of m values calculated from the number of failures of synaptic response observed in homonymous (upper) and heteronymous (lower) synapses. The EPSPs which showed no failure for about 200 trials are grouped in a class of > 5·5. Ordinates, percentage of total number of observations (forty-three) for homonymous and twenty-one heteronymous.

(Fig. 6*B*). The correlation was highly significant ($P < 0{\cdot}01$ by t-test), even though the data only covered a relatively narrow range of input resistances. From the relation shown in Figure 6*B*, the amplitude of unit EPSPs (v_1) may approximately be given by the formula,

$$v_1 \text{ (mV)} = 0{\cdot}06R \text{ (M}\Omega\text{)} + 0{\cdot}06,$$

where R is the input resistance.

The apparent lack of correlation between the v_1 and the motor axon conduction velocity (Fig. 6*A*), and hence, between the input resistance and the axonal conduction velocity, may lie in the nature of the microelectrodes employed in the present study. In order to improve the signal-to-noise ratio, only low impedance (5–10 MΩ) micropipettes were selected for all experiments. Possibly, penetration with these electrodes might have

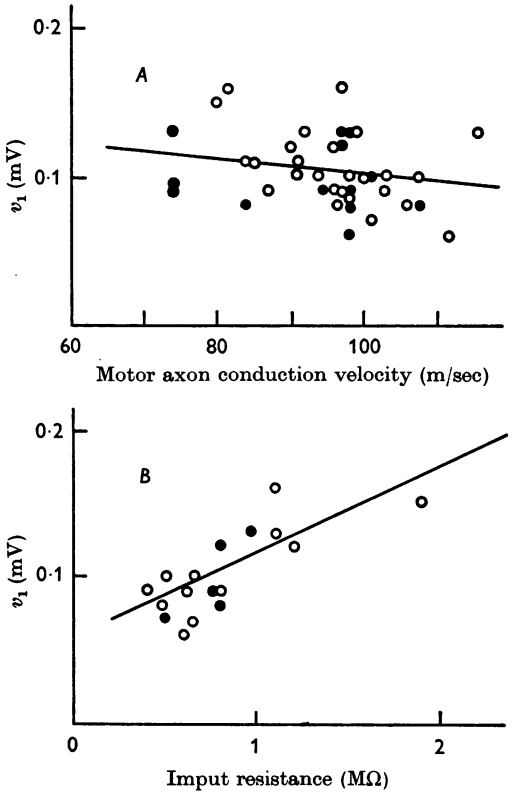

Fig. 6. *A*. Relation between the amplitude of unit EPSPs (v_1) and the axonal conduction velocity of motoneurones. *B*. Relation between the amplitude of unit EPSPs (v_1) and the input resistance of motoneurones. Open and filled circles are for homonymous and heteronymous synapses, respectively.

caused some injury to the motoneurones, especially to those with relatively small diameters. In addition, the limited number of observations on slow-conducting motoneurones (see Fig. 6*A*) might have made it difficult to detect the underlying correlation between the v_1 and the axonal conduction velocity of motoneurones. However, there is no doubt that the amplitude of unit EPSPs is directly related with the input resistance of motoneurones (Fig. 6*B*). From the results combined with those by Kernell (1966) and

Burke (1967*b*) it is suggested that high synaptic efficacy in relatively slow-conducting motoneurones is due to the large amplitude of unit EPSPs.

Since the mean amplitude of unit EPSPs is entirely dependent on the properties of the post-synaptic membrane (Katz, 1962), the v_1 in a given motoneurone would be approximately identical regardless of the afferent source (Blankenship & Kuno, 1968). However, it has been suggested that there is a strategic difference in location between the synapses formed by homonymous and heteronymous afferent fibres (Lloyd, 1946; Hunt, 1955). This suggestion has recently been supported by Jack & Porter (1966) who found that 'homonymous volleys tended to evoke EPSPs containing more of the rapidly rising components, whereas heteronymous volleys usually produced more slowly rising synaptic potentials'. In contrast to this notion, when the amplitude of unit EPSPs was plotted against the motor axon conduction velocity (Fig. 6*A*) or the motoneurone input resistance (Fig. 6*B*), the points for homonymous (open circles) and heteronymous (filled circles) EPSPs were distributed contiguously along a straight line without any distinct separation into two categories.

The above test might not be crucial, since the samplings of the synaptic responses in Fig. 6 were obviously biased in favour of synaptic responses close to the motoneurone soma (see above). An additional test is illustrated in Fig. 7 which shows monosynaptic EPSPs recorded from three medial gastrocnemius motoneurones (*a*, *b*, and *c*). In each motoneurone, the EPSPs were produced by stimulation of a single afferent fibre arising from the medial gastrocnemius muscle (homonymous) and of another fibre from the lateral gastrocnemius plus soleus muscles (heteronymous). The monosynaptic EPSPs evoked by about 200 consecutive stimuli applied to each afferent fibre were led into an averaging computer so that the average time course of the EPSPs elicited by the two different inputs could be compared. While the time-to-peak of the homonymous EPSP was appreciably shorter than that of the heteronymous EPSP in one motoneurone (*a*), the relation was opposite in two motoneurones, one of which is shown in *b*. In addition, there was no significant difference in time course between homonymous and heteronymous EPSPs in two other motoneurones (*c*). Furthermore, homonymous (forty-three) and heteronymous (twenty-one) EPSPs were observed in a total of sixty-four medial gastrocnemius motoneurones by stimulation of single afferent fibres. There was no significant difference in the average time-to-peak between homonymous and heteronymous EPSPs.

Convergence of afferent fibres on motoneurones. As shown in Fig. 1, a primary afferent fibre diverges into numerous branches in the spinal cord so that it is possible to record monosynaptic EPSPs from different moto-

neurones by stimulation of the same afferent fibre. In some experiments, one afferent fibre was found to make monosynaptic connexions with ten or more motoneurones (Table 1). However, a significant fraction of triceps surae motoneurones did not show any detectable monosynaptic EPSPs in response to stimulation of a given afferent fibre in the triceps surae nerve. For example, in expt. 1 of Table 1, a total of twenty-nine triceps surae (TS) motoneurones were recorded, but only eleven of them responded with

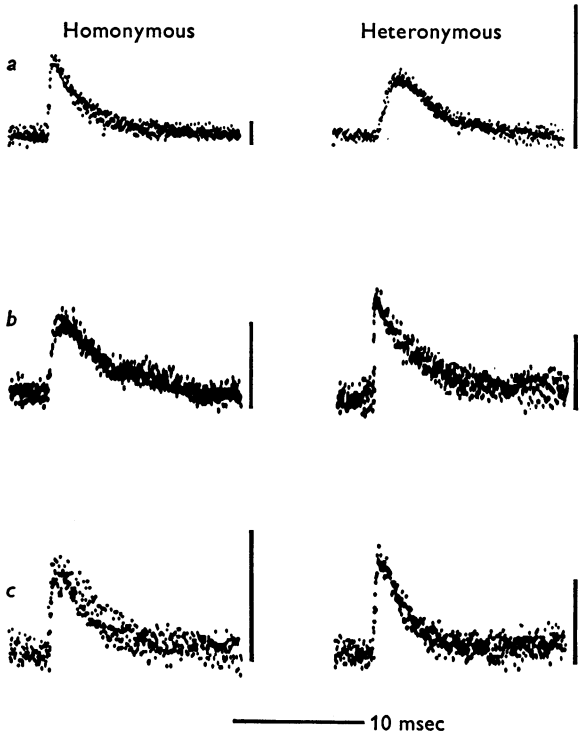

Fig. 7. Monosyanptic EPSPs evoked in three different medial gastrocnemius motoneurones (*a*, *b*, and *c*). by stimulation of single afferent fibres from homonymous and heteronymous muscles. Each trace comprises about 200 responses as summated by an averaging computer. Vertical calibrations, 0·2 mV.

monosynaptic EPSPs to stimulation of one afferent fibre arising from the medial gastrocnemius (MG) muscle. Therefore, in this particular experiment, the ratio of the motoneurones which receive synaptic connexion from the MG afferent fibre would be 37·9 % (11/29) of the total TS motoneurone pool. If a given afferent fibre makes synaptic connexions with TS motoneurones non-selectively, the percentage of homonymous and heteronymous synaptic connexions should be equivalent and be given by the percentage of synaptic connexion over the total TS motoneurones examined.

Of the twenty-nine TS motoneurones, twenty-two were found to belong to medial gastrocnemius (MG) motoneurones and seven to lateral gastrocnemius plus soleus (LGS) motoneurones. Of the twenty-two MG motoneurones, nine motoneurones showed monosynaptic connexion to the MG afferent fibre, while only two out of the seven LGS motoneurones had synaptic connexion with the MG afferent fibre. Thus, in this experiment the afferent fibre tends to make synaptic connexion with homonymous motoneurones (40·9 %) more than with heteronymous (28·5 %). Table 1 summarizes seven experiments, in each of which more than fifteen TS motoneurones were recorded and tested for the percentage of homonymous and heteronymous synaptic connexions. The average ratio of synaptic

TABLE 1. Distribution of primary afferent terminals within triceps surae motoneurone pool

Experiment	Type of afferent fibre stimulated	Motoneurones recorded			Motoneurones with synaptic connexion					
					TS		Homonymous		Heteronymous	
		TS (no.)	MG (no.)	LGS (no.)	Ratio	%	Ratio	%	Ratio	%
1	MG	29	22	7	11/29	37·9	9/22	40·9	2/7	28·5
2	MG	21	16	5	11/21	52·3	11/16	68·7	0/5	0
3	MG-a	17	7	10	12/17	70·5	5/7	71·4	7/10	70·0
	MG-b	17	7	10	2/17	11·7	2/7	28·5	0/10	0
	MG-c	17	7	10	3/17	17·6	0/7	0	3/10	30·0
4	LGS	19	16	3	3/19	15·7	2/3	66·7	1/16	6·2
5	MG	19	14	5	4/19	21·0	4/14	28·5	0/5	0
	LGS	19	14	5	5/19	26·3	2/5	40·0	3/14	21·4
6	MG	16	7	9	6/16	37·5	5/7	71·4	1/9	11·1
7	MG	16	13	3	5/16	31·3	4/13	30·8	1/3	33·3
	Average % of motoneurones with synaptic connexion					32·2	—	44·7	—	20·1

connexion from one afferent fibre was significantly greater for homonymous motoneurones (44 out of 101 motoneurones) than for heteronymous motoneurones (18 out of 89 motoneurones). From these results, it seems clear that when a number of afferent fibres are synchronously stimulated, monosynaptic EPSPs could be larger in a homonymous motoneurone than in a heteronymous motoneurone because of the larger number of afferent fibres converging on to the former.

DISCUSSION

Efficacy in homonymous and heteronymous synapses. Mendell & Henneman (1968) have shown that a single muscle afferent fibre makes monosynaptic connexions with almost all of the homonymous motoneurones. In contrast, the average ratio of homonymous motoneurones having synaptic connexion from a given afferent fibre was approximately 45 % in the present

study (Table 1). It is possible that the small synaptic response recorded by Mendell & Henneman (1968) with the aid of an averaging computer was not detected with any degree of certainty by our conventional recording technique. In fact, when an averaging device was employed in later experiments, it became evident that the average amplitude of 0·06 mV was approximately the limit of monosynaptic EPSP detected by our method. However, since the same technique was used throughout the present tests, there seemed no doubt that the relative ratio of monosynaptic connexions from one afferent fibre on to homonymous motoneurones is approximately twice as great as that on to heteronymous motoneurones.

In ventral root reflex discharges, Lloyd, Hunt & McIntyre (1955) have shown that 'transmitter potentiality' of an afferent fibre on spinal motoneurones varies widely but displays no distinct difference between homonymous and heteronymous monosynaptic responses. This is compatible with the present observations that there is no significant difference in m values between homonymous and heteronymous synapses. Furthermore, the amplitude of unit EPSPs as well as the time course of EPSPs is approximately identical in homonymous and heteronymous motoneurones. Thus, it is concluded that the convergence ratio of afferent fibres on a motoneurone is the only factor to distinguish the synaptic efficacy between homonymous and heteronymous reflex pathways.

Synaptic efficacy in fast- and slow-conducting motoneurones. It has been suggested (Kuno, 1964*a*) that the average amplitude of unit EPSPs in slow-conducting motoneurones is larger than that in fast-conducting motoneurones because of the high input resistances in the former (Katz & Thesleff, 1957). This suggestion is consistent with subsequent observations that slow-conducting motoneurones have lower threshold for the stretch reflex than fast-conducting motoneurones (Henneman *et al.* 1965) and that the input resistance is higher in slow-conducting motoneurones (Kernell, 1966; Burke, 1967*b*). In addition, Burke (1968) has found that there is a positive correlation between the input resistance of motoneurones and the average amplitude of EPSPs evoked by single afferent impulses. From the present analysis, it seems clear that this relation is based on the positive correlation between the input resistance of motoneurones and the amplitude of unit EPSPs (Fig. 6*B*). Since there is no correlation between the m value and the axonal conduction velocity or the input resistance of motoneurones, the high synaptic efficacy in slow-conducting motoneurones can only be attributed to the large unit EPSPs as the result of the high input resistance.

Significance of m values in synaptic efficacy. There was a wide variation in the m value of monosynaptic EPSPs produced by stimulation of a single afferent fibre (Kuno & Miyahara, 1969). However, the m values were not

correlated with other functional parameters, such as the type of motoneurone recorded, the type of afferent fibre stimulated and the afferent source, i.e. homonymous or heteronymous. Since the m value depends entirely on the properties of the presynaptic terminals (Katz, 1962), it is conceivable that the m value may be related to the structure of the presynaptic terminals. Suggestive evidence for this notion has been provided recently by the high m values of monosynaptic EPSPs recorded from neurones in Clarke's column (Eide, Fedina, Jansen, Lundberg & Vyklický, 1967; Kuno & Miyahara, 1968*a*), which coincides with the presence of giant synaptic contacts on these neurones (Szentágothai & Albert, 1955). In this respect, it is rather surprising that the m value of EPSPs in spinal motoneurones shows such wide variation, since the presynaptic terminals on the motoneurone are relatively uniform in size (Haggar & Barr, 1950; Wyckoff & Young, 1956; Illis, 1964; Gelfan & Rapisarda, 1964). It is suggested that the variation of the m value is due to the difference in the number of afferent terminal branchings on a motoneurone (also, see Kuno, 1964*a*; Burke & Nelson, 1966). Since the large m values are associated with high degree of non-linear summation (Kuno & Miyahara, 1969), it is likely that the multiple synaptic contacts arising from one afferent fibre are closely located on the same dendrite. It should also be noted that in a given monosynaptic pathway, the m value is altered by the frequency of afferent impulses (Kuno, 1964*b*). In addition, the m value increases after tetanic afferent stimulation and is decreased by the conditioning volleys which lead to presynaptic inhibition (Kuno, 1964*b*). Thus, the mean quantum content (m) may be considered as the dynamic determinant of synaptic efficacy in spinal motoneurones, while the amplitude of unit EPSPs (v_1) and the number of afferent fibres (N) converging on a motoneurone may determine the efficacy in static conditions.

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