

MONOSYNAPTIC REFLEX RESPONSE OF INDIVIDUAL MOTONEURONS AS A FUNCTION OF FREQUENCY

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From time to time questions arise concerning the behavior of motoneurons in some circumstance of reflex activation that cannot be answered by observation of a population of motoneurons. It is then appropriate to resort to the study of individual members of the population. Even without the pressure of necessity it sometimes happens that the observation of individuals increases one's grasp of the population's workings. To the end that study of individuals will yield an adequate picture of the population behavior one assembles a synthetic motoneuron pool after the fashion of Lloyd and McIntyre (9) and whenever possible devises some test by means of which to compare behavior of the synthetic pool with that of a natural motoneuron pool subjected to similar conditions of excitation. The experiments to be discussed have examined the relation between frequency and monosynaptic reflex response in an assemblage of individual motoneurons constituting a synthetic motoneuron pool.

Reconstituting Pool Behavior.—In a synthetic motoneuron pool constructed of individuals responding to monosynaptic reflex afferent volleys presented at some low repetition rate some individuals respond to every trial and are designated as displaying a firing index (Fi) of 100. Others, and these account for some 20 to 30 per cent of the pool (9), display intermediate firing indices. Still others do not respond and hence fall into the $Fi = 0$ category. In the present experiments sequential examination of isolated motoneurons was practiced until an intermediate zone of the same dimensions as that originally found by Lloyd and McIntyre (9) was obtained. By the time this was done a somewhat smaller number of $Fi = 100$ motoneurons had been encountered. The number of $Fi = 0$ motoneurons is not significant for a decision was made not to enter all the $Fi = 0$ motoneurons that could be identified with the aid of post-tetanic potentiation of response, but that did not respond during stimulation at any frequency in the range under study.

For the purpose of assembling the synthetic motoneuron pool a stimulus repetition rate of 30 per minute was used, this being the nearest practical rate to that of the original series, which was 25 per minute. To the left of Fig. 1 is represented, by the solid line plot, the behavior, with respect to firing indices,

of the present synthetic motoneuron pool. For comparison there is plotted by means of the broken line the original synthetic pool of Lloyd and McIntyre adjusted for difference in the number of $Fi = 100$ neurons. The comparison shows the present pool to be relatively a little short in the range from $Fi = 70$

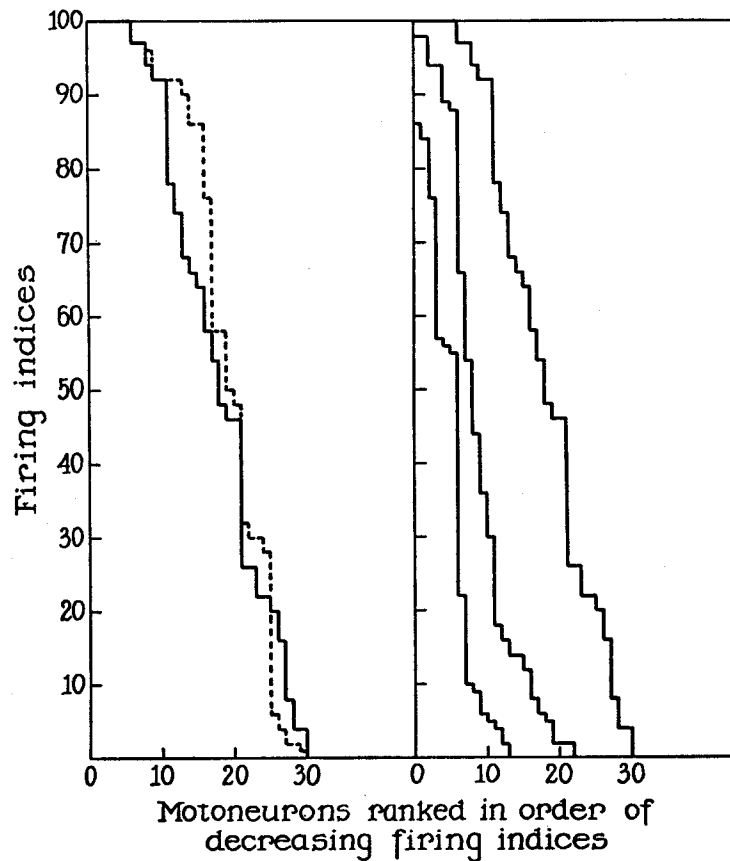


FIG. 1. On the left the solid line plot ranks the individual members of the synthetic motoneuron pool in order of decreasing firing indices. For comparison the broken line represents the original synthetic pool of Lloyd and McIntyre (9) adjusted for difference in number of $Fi = 100$ motoneurons. On the right is represented the response behavior of the synthetic pool in circumstances of varied stimulation frequency.

to $Fi = 90$ and a little high in the range from $Fi = 50$ to $Fi = 70$. Nevertheless all grades are represented and the differences are not great.

From data of the sort contained in Fig. 1 it is possible to calculate in a manner earlier described (9) the average discharge zone which gives the ficti-

tious monosynaptic reflex in the given conditions of activation. To the right of Fig. 1 are three plots that characterize the behavior of the present synthetic pool with respect to firing indices at three frequencies of stimulation. These plots, reading from left to right, represent behavior at 10 per second, 2 per second, and 30 per minute respectively. From the information contained in these plots, and others representing other frequencies, the mean fictitious monosynaptic reflex of the synthetic pool was calculated for a variety of fre-

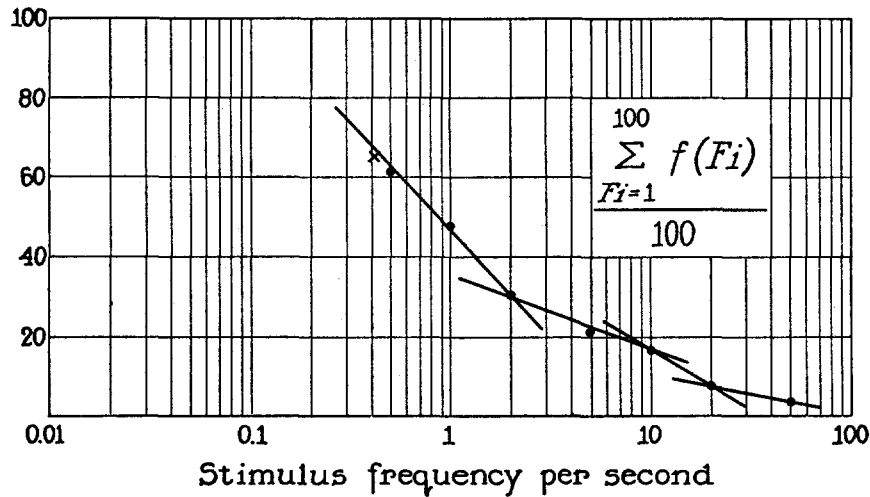


FIG. 2. Average discharge zone (the fictitious monosynaptic reflex) of the synthetic motoneuron pool is here plotted as a function of frequency. Cf. reference 11 for natural curves with which this may be compared.

quencies. The result is shown in Fig. 2 which relates amplitude of the mean fictitious monosynaptic reflex:

$$\frac{\sum_{F_i=1}^{100} f(F_i)}{100}$$

to frequency.

Since the relation displayed in Fig. 2 is a close match for the type of relation found when natural pools are the object of study (reference 11, Figs. 1, 4, 5), one may suppose that the method of sequential examination again has proven adequate to secure representative sampling as it has in the study of muscle afferent fibers (3), of motoneurons in the circumstance of post-tetanic potentiation (9), and of motoneurons with respect to the relation of monosynaptic reflex output to afferent input (4).

Some Examples of Individual Behavior.—Fig. 3 presents the frequency- F_i relations of five selected individual motoneurons. Before discussing them it is well to bring to mind the fact that postsynaptic subnormality inevitably must limit the firing indices attainable at higher frequencies. Assuming for the moment that the limiting response frequency is 10 per second, based upon an effective subnormal period of 100 msec., then the broken line in Fig. 3 will express the limitation upon firing indices at frequencies between 10 and 100 per second. Actually the limitation is not quite so stringent (*cf.* Fig. 7)

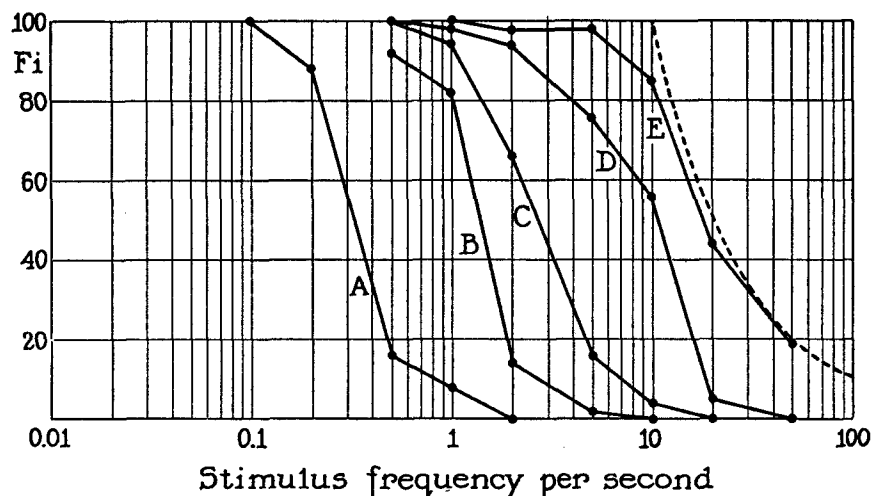


FIG. 3. Frequency-firing index relations of five selected individual motoneurons in the frequency range below 50 per second.

but the value chosen for construction of Fig. 3 is as good as another for the purpose.

The frequency- F_i relation for most of the neurons examined lay to the left of that for neuron C of Fig. 3, and of these most did not at any of the frequencies examined approach $F_i = 100$. A number yielded relations resembling that for neuron 3E. The type of frequency- F_i relation exhibited by neuron 3D according to present experience is unusual. Thus although the categorization is too rigid it is possible in the first approximation to describe behavior in terms of two typical sorts of neurons: those that behave in a manner rather like neuron 3B and those that behave as neuron 3E. According to previous experience one would say that these neurons, 3B and 3E differ in the transmitter potentiality of their monosynaptic afferent fiber connections (9, 10).

By increasing stimulus frequency neuron 3B, and others of its kind, are brought to $F_i = 0$ at frequencies below that at which postsynaptic subnor-

mality could influence the issue. Otherwise stated transmitter potentiality of the (maximal) afferent volleys is sufficiently low that neuron 3B and kind are removed from the discharge zone by operation of the low frequency (or enduring) depression mechanism. Whilst neuron 3E and kind also suffer from low frequency depression it is quite clear that a major factor limiting response is the high frequency depression due to subnormality.

If now one considers the frequency-amplitude relations for the natural pool monosynaptic reflexes illustrated in Fig. 5 of an antecedent paper (11), it may be realized that the difference between the relations described by curve A and by curve B of that figure may be explained simply by supposing that the two reflexes concerned involved differing proportions of neurons displaying the "neuron 3B type" of behavior and the "neuron 3E type" of behavior. Thus mean reflex amplitude at a stimulation frequency of, say, 10 per second may be considered as giving a rough estimate of the relative number of 3E type motoneurons involved in the particular population monosynaptic reflex response under observation. Furthermore, in experiments utilizing the two shock technique and a variable conditioning volley (*cf.* reference 11, Fig. 10), it is presumably the existence of 3E type motoneurons that places a ceiling on the degree of depression that can result from still incrementing conditioning volleys.

It should be noted that the difference in behavior represented by neuron 3B and neuron 3E is not the result of difference between one preparation and another for both types of frequency- F_i curves were readily obtained in one and the same preparation.

Depression and Transmitter Potentiality.—Degree of depression is not a simple function of transmitter potentiality. If the depressing action of an afferent volley impinging upon a motoneuron were simply related to the transmitter potentiality of that volley at that motoneuron then those motoneurons that are powerfully driven should be powerfully depressed and those lightly driven should be only slightly depressed. The end result would be that each individual motoneuron examined would display a frequency-firing index relation much like that of all the others, which manifestly is not the case.

A suitable accounting for the differences in behavior of individual motoneurons is forthcoming if one supposes that degree of depression may be related solely to the number of active presynaptic endings on any given motoneuron just as is facilitation of response in convergent pathways (4). Then, as shown by Hunt (4), with transmitter potentiality related not only to number but to aggregation of active endings the degree of depression could to a considerable extent vary independently of transmitter potentiality. For instance, a motoneuron receiving relatively few monosynaptic connections in a highly aggregated state might yield evidence of its monosynaptic connections possessing a high degree of transmitter potentiality and at the same time

be little depressed in the low frequency range, as is neuron E of Fig. 3. Conversely, a motoneuron fitted with a goodly number of endings, highly dispersed, might have a low firing index and be severely depressed in the low frequency range.

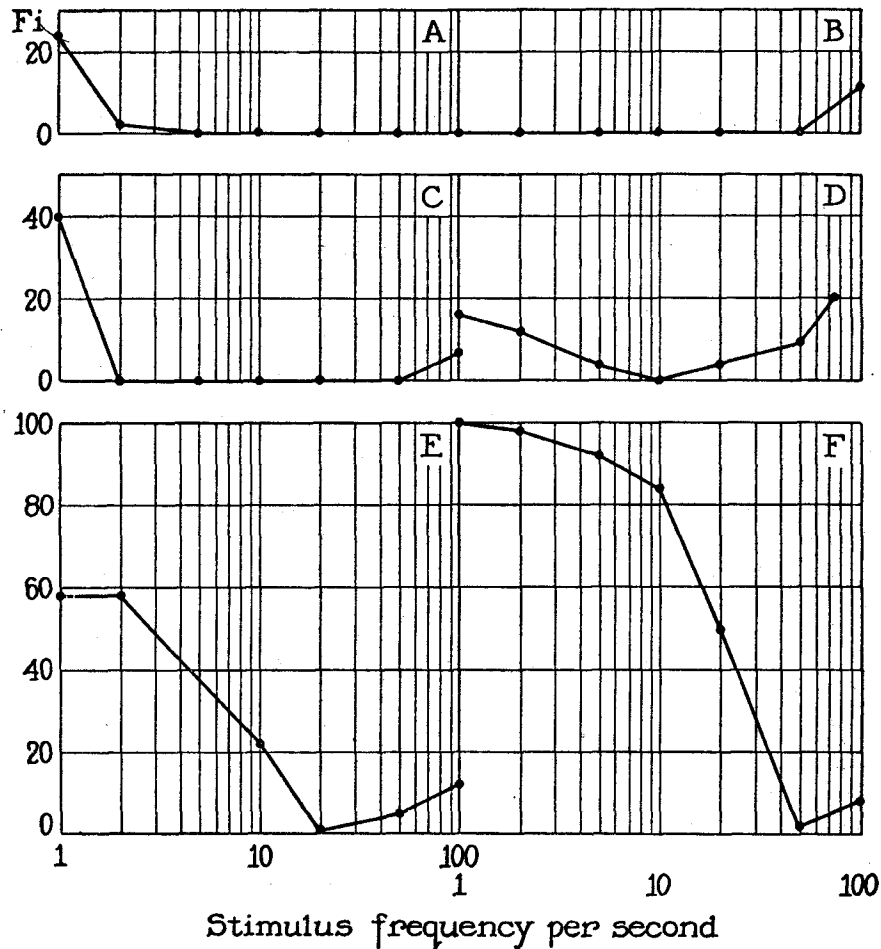


FIG. 4. Frequency-firing index relations of six individual motoneurons in the frequency range between 1 and 100 per second.

Further Examples of Individual Behavior.—Fig. 4 presents instances of individual motoneuron response at frequencies varied between 1 and 100 per second to illustrate certain details concerning temporal summation, high frequency depression (subnormality), and low frequency depression. Neurons 4,

A, B, C, D had been depressed to $Fi = 0$ at a frequency of 10 per second from which it follows that high frequency depression due to postsynaptic subnormality could not have been a factor in these instances of depression. Neuron 4E did have its response incidence curtailed by subnormality in a manner that will be discussed in connection with Fig. 5. For the moment it is necessary only to know that subnormality influenced the issue. Neuron 4F was very obviously and decidedly influenced by subnormality, its frequency- Fi relation, like that of neuron 3E, approaching the subnormality imposed limit.

Subnormality unquestionably placed a ceiling on the high frequency increment in firing index displayed by neuron 4D, for at frequency of 75 per second it was responding on the average every 66.5 msec., but subnormality cannot be invoked to account for any feature of the frequency- Fi relation at lower frequencies. There is no necessity to assume that subnormality placed a ceiling upon high frequency response of the other neurons. Neuron 4A stands in exemplification of the fact that an increment in firing index need not be realized as frequency increases to 100 per second.

If single shock or low frequency response of a natural pool has been suppressed by narcosis (6) or does not occur, as is ordinarily the case in heteronymous pathways (7, 10), one finds that frequencies of approximately 70 per second and higher are requisite for the appearance, by temporal summation, of monosynaptic reflex discharge. In the study of individuals one can, in addition, select for study those that are in the $Fi = 0$ category at low frequencies of stimulation, and by so doing achieve the same condition. Such motoneurons not surprisingly, behave in the same way as does the natural pool that is unresponsive at low frequency. Neuron 4B displays this sort of behavior.

Among neurons that do respond at low frequencies, or to single shocks, one may find that a minimum degree of response is realized at a frequency approximating 10 per second *provided* that subnormality is not a factor in determining response. In exemplification, response incidence of neuron 4D declines progressively as frequency increases from 1 to 10 per second, and increments progressively with further increase in frequency. Neuron 4C is depressed to an extent that the frequency of maximal depression cannot be defined.

An Incrementing Phase of Enduring Depression.—In an antecedent paper (reference 11, Fig. 8) the time course of low frequency, or enduring, depression was plotted for the interval beginning approximately 100 msec. after monosynaptic reflex response and ending with the apparent decay of depression to insignificance at 20 seconds. The course of low frequency depression during the first 100 msec. could not be charted because of interference by subnormality of motoneurons. By the use of properly selected individuals (such as neuron 4D) the impact of subnormality can be avoided and the results obtained show that the low frequency, or enduring depression dis-

plays an incrementing phase to reach maximum at approximately 10 per second or, in terms of stimulus intervals, 100 msec.

In the light of the present findings it is of interest to consider certain responses recorded by Alvord and Fuortes (1) and published in their Fig. 4. On the left side of that figure are simultaneous recordings from the homonymous and heteronymous fractions of triceps at stimulus frequencies of 1, 10, 50, 100, and 150 per second. The heteronymous path requires for discharge a stimulation frequency in excess of 50 per second but presumably less than 100 per second. On the other hand the homonymous path that responds at low (1 per second) frequency and at high (50 per second and higher) frequency displays a minimum approaching extinction of response at 10 per second. Although Alvord and Fuortes were not concerned with the problem of depression their results concur with those here presented in showing that frequencies in excess of 60 per second are requisite for actual temporal summation to occur, but that discharge minimum may be at 10 per second: in short that temporal summation leads into a phase of incrementing depression.

Influence of Subnormality upon the Frequency- F_i Relation.—Each motoneuron that is less influenced than some other motoneuron by low frequency depression is *pari passu* more influenced by high frequency depression. Neurons 4D, 4E, and 4F constitute a series to illustrate the influence upon the course of high frequency response increment of variation in the relative contribution to depression by the low and high frequency processes. Neuron 4D is not influenced by subnormality, neuron 4E is moderately influenced, and the response of neuron 4F is largely determined by subnormality. Each of these three neurons displays a high frequency increment in response incidence, but the frequency at which the minimum response is realized shifts progressively upward as subnormality becomes an increasingly important cause of depression.

Fluctuation and the Frequency- F_i Relation—How Subnormality Can Influence the Issue at Low F_i .—The occurrence of intermediate firing indices depends upon excitability fluctuation in the spinal cord (9). At all frequencies of stimulation above 1 per second neuron 5 (Fig. 5) displayed intermediate firing indices. Furthermore it is obvious from the records that firing index decreased with increasing frequency. At stimulus frequencies 2, 5, and 10 per second subnormality could have no influence on the ability of the neuron to respond. Therefore response is determined by the level of low frequency depression relative to excitability fluctuation.

When subjected to a stimulus frequency of 20 per second the firing index of neuron 5 was a low value due largely to low frequency depression. Nevertheless, within each burst of response the neuron, with one exception, was unable by reason of subnormality to follow the stimulus frequency but could in many instances respond at the first submultiple. At a stimulus frequency

of 50 per second neuron 5 did on a few occasions respond successively at intervals of 80 msec. although its firing index was considerably lower than at a frequency of 20 per second. When frequency of stimulation was increased to 100 per second the neuron was capable on many occasions of responding 60 msec. following prior response, undoubtedly aided by temporal summation. Except for the regular rhythmicity of fluctuation, which is interesting,

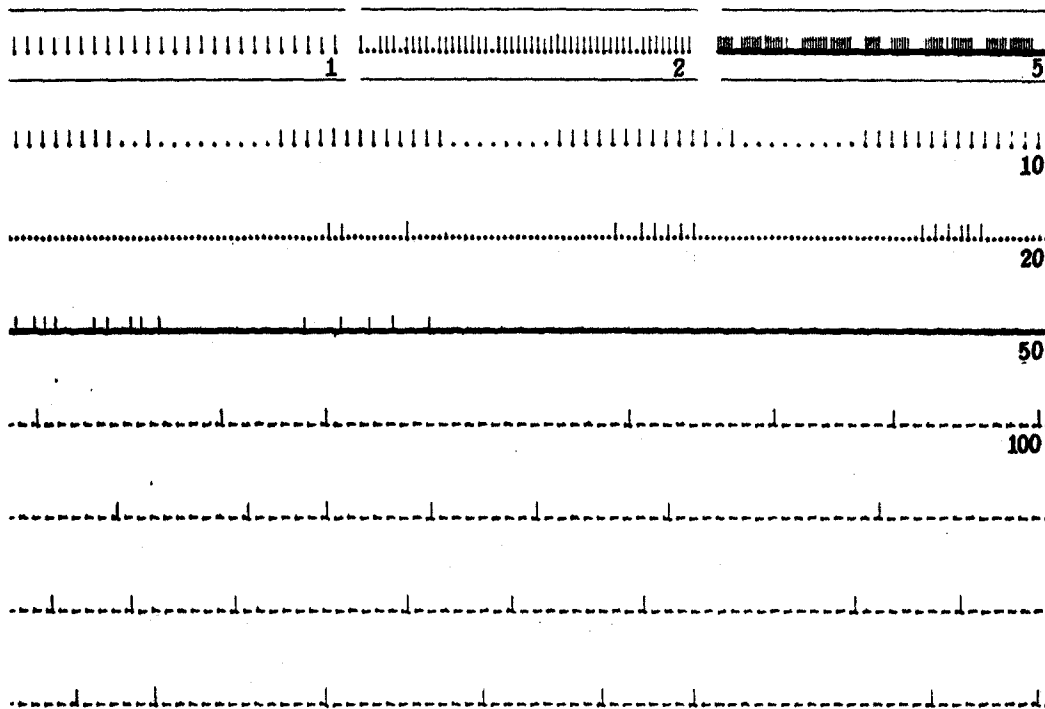


FIG. 5. Responses of a motoneuron at stimulation frequencies varied between 1 and 100 per second. Paper speed increased ten times between 5 and 10 and again between 50 and 100.

unusual, but incidental to the present main point at issue, neuron 5 exemplifies in a simple and usual way the fact that subnormality can influence response at very low firing indices.

Fluctuation and the Origins of Rhythm.—At frequencies below 10 per second rhythm of response depends upon stimulus frequency. So long as the firing index is 100 the rhythm of response is unbroken whether frequency be as low as 1 per second (Fig. 5), or lower, or as high as 10 per second (Fig. 6). The assertion (1) that motoneurons do not fire rhythmically at a stimulus frequency of 10 per second is not confirmed in the present study and indeed

appears to be the consequence of generalization of findings obtained in limited experimental conditions. At whatever stimulus frequency they occur in the range below 10 per second interruptions of rhythmic firing result solely from excitability fluctuation (9).

In the frequency range above 10 per second rhythmic firing may or may not be present and when it occurs may do so in bursts. In this range, however, the rhythm is some submultiple of the stimulation frequency. At the

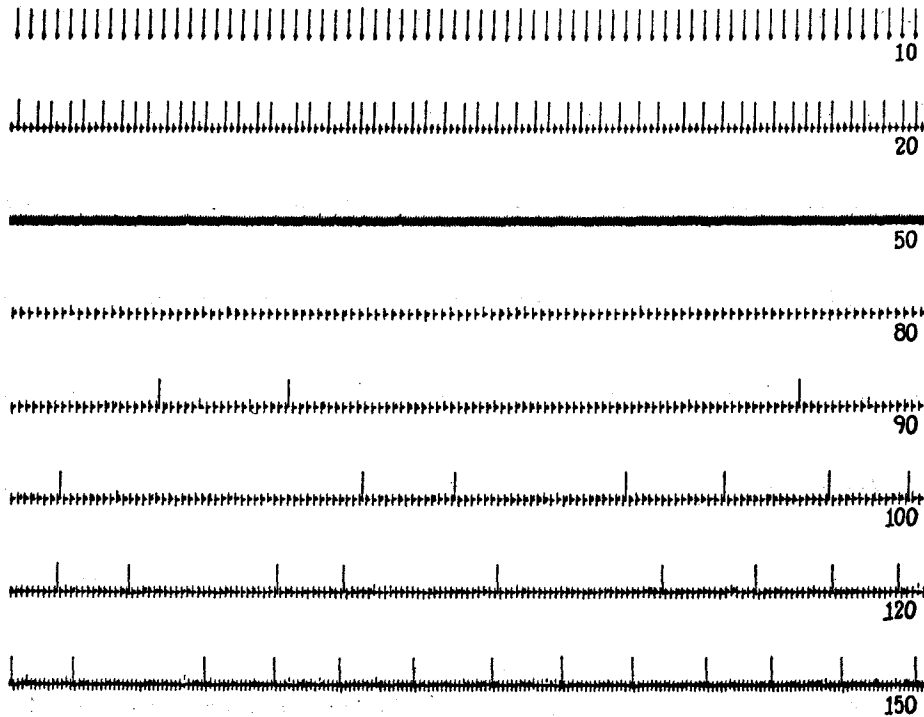


FIG. 6. Responses of another motoneuron at stimulation frequencies varied between 10 and 150 per second. Paper speed increased five times between 50 and 80.

high frequencies of stimulation the steady state level of excitability increases with frequency due to temporal summation (6). As it does so the influence of temporal fluctuation is progressively lessened. In consequence response appears less in the form of bursts and more in the form of regular discharge. Stimulated at a frequency of 100 per second or higher a motoneuron, such as neuron 6 (Fig. 6), may respond just as frequently as it does at 10 per second, but the rhythm is less precise. The reason is simple: a motoneuron receiving volleys each 100 msec. (*i.e.* at a frequency of 10 per second) has no alternative but to respond precisely on the 100 msec. interval, or not to re-

spond, depending upon the instantaneous excitability level in fluctuation. When stimulation frequency is 100 per second the motoneuron is free to respond not only precisely on the 100 msec. interval but also after 90 or 80 msec. as well as after longer intervals depending upon fluctuation. The higher the steady state excitability level established by temporal summation and the less the influence of fluctuation in consequence, the more regular response becomes and the closer response approaches the limit imposed by subnor-

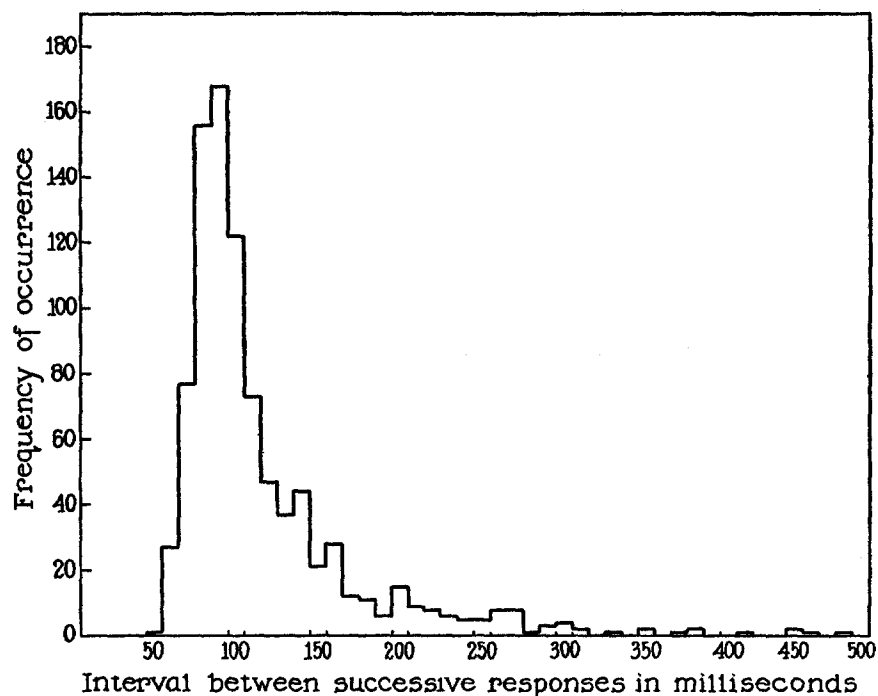


FIG. 7. The frequency of occurrence of intervals between successive responses to a train of monosynaptic reflex afferent volleys at a frequency of 100 per second.

mality. One concludes that the only condition for rhythmic response is that random excitability fluctuation must not influence the issue. Given that condition frequency of rhythmic response is determined by stimulus frequency at low frequencies and at high frequencies by subnormality. Fig. 7 contains a histogram of the frequency distribution of intervals between successive responses at a stimulus frequency of 100 per second. It serves to illustrate graphically the influence of fluctuation upon the ability of neurons to respond rhythmically. In all 915 responses of 10 motoneurons are represented. The distribution is markedly skewed.

Given a certain mean level of excitability and afferent volleys of constant

strength then in total absence of effective influence by fluctuation the motoneurons would respond regularly at intervals of, say, 90 msec. Now, given a slight influence by fluctuation, one can see that a neuron might on some occasions respond after 80 msec. and on some other occasions after 100 msec. depending upon the direction of fluctuation from the mean excitability level. One might expect a motoneuron subjected to slight influence by fluctuation to yield a Gaussian distribution of response intervals. Next, given a greater influence by fluctuation, and this apparently is the actual experimental situation, it will be seen that response of the neuron during fluctuation in the direction of enhanced excitability must inevitably reach a limit imposed by subnormality, which accounts for the form of the distribution toward the short interval side of the modal value. During fluctuation in the direction of decreased excitability there is no upper limit imposed upon the duration of response interval beyond that inherent in the quality of fluctuation itself which accounts for the form of the distribution to the long interval side of the modal value. Otherwise put the degree of skewness in the distribution of response intervals is a reflection of the degree to which motoneuron response is subject to fluctuation.

According to Fig. 7 the modal response interval is 90 msec., which would correspond to a rhythm of approximately 10 per second. Ten per second rhythm is not at all an uncommon finding in activity of the central nervous system. It could result from the occurrence of motoneuron discharge (subnormality) or occur independently of motoneuron discharge (inherent rhythmicity). Fig. 7 provides suitable evidence from which to choose that alternative which is of concern in the workings of the monosynaptic reflex pathway. The absence of prominent peaks in the distribution of response intervals at multiples of 90 msec., the most probable interval, indicates that response intervals are not determined by a rhythmic excitatory process existing independently of the occurrence of motoneuron response. This is not to deny to motoneurons the property of rhythmicity which is well established as a fundamental property of excitable tissue (*cf.* for instance reference 2): it need only mean that the temporally random fluctuation characteristic of spinal cord responsivity (9, 12) is of a magnitude such as to dominate behavior. This also is not to deny that 10 per second rhythm, or indeed rhythm at other frequencies can in other situations be the consequence of inherent rhythmicity.

On Shock Response Interval.—At no time has response of a motoneuron subjected to high frequency afferent bombardment occurred either out of relation to the afferent volleys or with a latency that is not appropriate for short latency monosynaptic reflex discharge. This is in accord with some of the findings of Alvord and Fuortes (1), but not with others. The essential conditions under which Alvord and Fuortes observed a lack of strict relation

between shock and response were stimulation with weak shocks, or of heteronymous afferent fibers, in decerebrate preparations. Since they considered only results obtained from preparations that displayed extensor rigidity it may be assumed that the motoneurons studied (gastrocnemius) were subjected to a heavy excitatory bombardment from supraspinal centers.

The question now is whether random discharge to high frequency iterated stimulation, when it does occur, does so as the result of action intrinsic to the monosynaptic reflex pathway as is, in essence, the proposal of Alvord and Fuortes, or whether impingement from sources extrinsic to the monosynaptic reflex pathway controls the timing of discharge. The mere fact that monosynaptic response of motoneurons at high stimulation frequencies has not become random with respect to afferent volleys in spinal and anesthetized preparations and has in the rigid decerebrate preparations of Alvord and Fuortes is presumptive evidence that the random and extrinsic bombardment that is essential for the development of decerebrate rigidity is likewise the essential ingredient leading to random discharge.

In agreement with Alvord and Fuortes one may believe that it is difficult to bring random bombardment such as that of decerebrate rigidity under experimental control. However, it is possible to introduce a controlled asynchronous bombardment from a source extrinsic to the monosynaptic pathway itself and to combine this with monosynaptic reflex volleys possessing any chosen degree of transmitter potentiality for a given motoneuron under observation. A means for doing this is to stimulate the brachial plexus which in action provides to the motor nucleus of gastrocnemius, for instance, a dispersed internuncial excitatory barrage that waxes and wanes over a considerable interval of time and which may of itself, at the peak of intensity, secure some motoneuron discharge (5, 8). Monosynaptic reflex afferent volleys then are delivered so as to arrive after the onset of internuncial bombardment and before the onset of long spinal reflex discharge, if such indeed does occur.

When all this is done (10), it is found occasionally that the combination of heteronymous monosynaptic reflex afferent volleys and long spinal reflex barrage, each severally ineffective, may lead to instability of interval between monosynaptic reflex afferent volley and response. Prior tetanization of the monosynaptic reflex afferent pathway leads to increased incidence of response and to fixation of response in time relative to the monosynaptic reflex afferent volleys. All responses to homonymous and heteronymous afferent volleys potentiated by prior tetanization, or not, as the case may be, but secured in the absence of long spinal reflex barrage, are linked in appropriate short latency reflex timing with respect to afferent volleys. In other words the presence of extrinsic dispersed bombardment appears in the experiments of Lloyd and McIntyre, and would appear in those of Alvord and Fuortes, to be the essential factor in randomization of response relative to such monosynaptic

reflex afferent volleys as are presented to the motoneurons. A further important aspect of the experiments of Lloyd and McIntyre for purposes of the present discussion is that the randomization of response relative to the monosynaptic reflex volleys that occurred when long spinal reflex barrage was available to the motoneurons did so at a repetition rate of 25 per minute. Thus, not only does one find that random extraneous bombardment apparently is an essential factor in randomization of response with respect to monosynaptic afferent volleys, but one also finds that temporal summation, by high frequency stimulation, is not essential. There is, therefore, no reason to propose (*cf.* reference 1) that the agency responsible for temporal summation in the monosynaptic reflex pathway is capable by summation during high frequency afferent stimulation of becoming a transmitting agency in its own right. This in turn leads one to conclude that the sustained reflex of Alvord and Fuortes (1) reveals nothing distinctive concerning the reflex mechanism and that such distinctions as have been drawn between sustained reflexes and unsustained reactions are artificial and unjustified.

Another Factor in Depression.—All the frequency dependent variations in mean monosynaptic reflex amplitude of pool responses that have been encountered (11, 6) and most of the behavior of individual motoneurons can be accounted for by the assumption of two processes: (1) subnormality, that limits response at high frequencies; and (2) a process that initially is facilitatory, that reverses at approximately 15 msec. to become depressive, that reaches maximum depressive action at approximately 100 msec., and that then dwindles to insignificance at about 20 seconds. Occasionally an individual motoneuron behaves in a manner that is not completely accounted for by the operation of these two processes. Neuron 4A is one such, also in lesser degree neurons 5 and 6. All three present the same problem.

At a stimulus frequency of 5 per second neuron 4A is depressed to the point that firing index is zero. It remains so depressed at all higher frequencies. Obviously subnormality plays no role in the behavior of neuron 4A since it is completely unresponsive. In the circumstance one would expect neuron 4A to enter the discharge zone by virtue of temporal summation at a stimulus frequency of 100 per second, but it does not. Such a variety of possible explanations for this sort of behavior exists without experimental basis for preference that one can do little more at this time than list some of the more obvious.

1. In this upper range of frequencies influences traceable to group IB or group II may be more effective than other experiments would lead one to suppose (11), or it may be that those influences largely masked in pool responses can be revealed by certain individual units.

2. Although a unit under study may not be responding, and hence subject to subnormality, others about it certainly are. Since the sequelae of discharge by some motoneurons may influence responsiveness of others (13) the unit in question may be giving expression to that form of influence.

3. A block may develop in some presynaptic fibers during repetitive stimulation at relatively high frequencies.

SUMMARY

An assemblage of individual motoneurons constituting a synthetic motoneuron pool has been studied from the standpoint of relating monosynaptic reflex responses to frequency of afferent stimulation.

Intensity of low frequency depression is not a simple function of transmitter potentiality.

As frequency of stimulation increases from 3 per minute to 10 per second, low frequency depression increases in magnitude. Between 10 and approximately 60 per second low frequency depression apparently diminishes and subnormality becomes a factor in causing depression. At frequencies above 60 per second temporal summation occurs, but subnormality limits the degree of response attainable by summation.

At low stimulation frequencies rhythm is determined by stimulation frequency. Interruptions of rhythmic firing depend solely upon temporal fluctuation of excitability. At high frequency of stimulation rhythm is determined by subnormality rather than inherent rhythmicity, and excitability fluctuation leads to instability of response rhythm. In short, whatever the stimulation frequency, random excitability fluctuation is the factor disrupting rhythmic response.

Monosynaptic reflex response latency is stable during high frequency stimulation as it is in low frequency stimulation provided a significant extrinsic source of random bombardment is not present. In the presence of powerful random bombardment discharge may become random with respect to monosynaptic afferent excitation provided the latter is feeble. When this occurs it does so equally at low frequency and high frequency. Thus temporal summation is not a necessary factor. There is, then, no remaining evidence to suggest that the agency for temporal summation in the monosynaptic system becomes a transmitting agency in its own right.

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