

## TEMPORAL SUMMATION IN RHYTHMICALLY ACTIVE MONOSYNAPTIC REFLEX PATHWAYS

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Problems of spatial summation in short latency monosynaptic reflex transmission have attracted considerable attention in recent years (14, 5, 18, 15, 16, 4). Much of the experimental effort directed toward these problems has been concerned with the relation between input and output and has centered about the two propositions: that the actions at motoneurons of monosynaptic reflex afferent volleys are in degree related solely to the number of active endings involved irrespective of location upon the postsynaptic soma (2, 18, 15, 16) or, alternatively, that location of active endings each relative to the others is an important determinant of synaptic efficacy (14, 5, 4). The most critical evidence now available (4) reaffirms the importance of location and is unequivocally in support of the concept that a brief synaptic action displaying a relatively sharp spatial decrement is responsible for generation of short latency monosynaptic reflex discharge.

Nevertheless, the elements that enter into synapsis, both presynaptic (11, 8) and postsynaptic (2), display enduring electrical change of a sort associable with excitation, and the facilitation of action in the simple pathway is known to have a time constant approximating 4 msec. (6) which is comparable with that of the electrical changes noted. Granting certain assumptions such processes at the synapsis might reasonably be supposed to provide a basis for temporal summation. Indeed the suggestion has been made that "processes similar to Eccles's (1946) 'synaptic potential' or Lloyd's (1946) 'residual facilitation' " (1) could satisfy the requirement for temporal summation in the monosynaptic reflex pathway. However, there exists no evidence to link temporal summation with the process underlying residual facilitation<sup>1</sup> and one is free to make what assumptions one chooses. The experiments to be discussed are presented with the aim of remedying this situation.

<sup>1</sup> Granit (3) has applied the term "residual facilitation" to the increment in action, and response, that follows a bout of high frequency stimulation, namely to post-tetanic potentiation (7). Likewise the temporal summation of which he speaks is related to the process underlying potentiation, not to that underlying residual facilitation as the term was originally and is here used. The terminology as here used may not be the best that can be devised, but it does have the merit of giving different names to different things.

Experimental arrangements in general have been those described in the antecedent paper (13), with the important exception that the majority of preparations were narcotized, usually deeply, with nembital, this for a purpose.

The records of Fig. 1 illustrate monosynaptic reflex responses, or the absence of them, when trains of monosynaptic reflex afferent volleys are engendered, at the indicated frequencies, in the nerves of triceps surae. Recording was from the first sacral ventral root. The preparation was narcotized to the point that

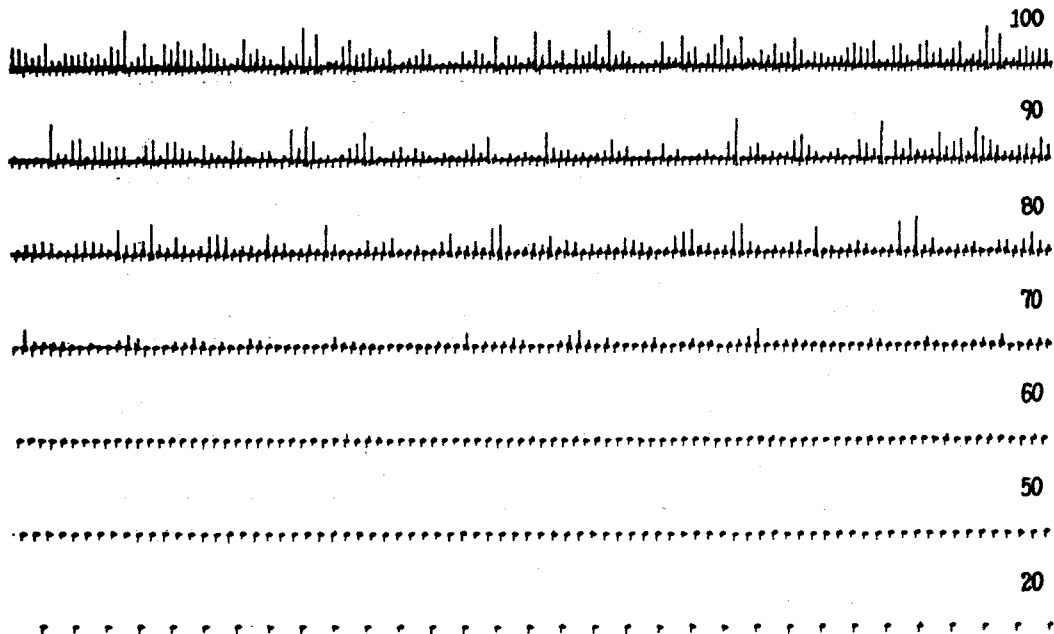


FIG. 1. Monosynaptic reflex behavior of tricipital motoneurons at various frequencies of afferent stimulation, which latter are indicated at the right in stimuli per second. Low frequency response suppressed by nembital.

single, or low frequency, supramaximal group I afferent volleys did not elicit any monosynaptic, or for that matter polysynaptic, reflex. It is evident from the recordings that some relation exists between frequency and the "amount" of monosynaptic reflex realized at frequencies above 60 per second. The problem is to define that relation.

An initial step in analysis was to determine the mean steady state monosynaptic reflex amplitude at each of the various frequencies of stimulation employed. Fig. 2 contains a plot relating mean monosynaptic reflex amplitude to frequency from an experiment in which response at frequencies from 0.2 per second to 100 per second was examined. For the immediate purpose mean

amplitude has been expressed in per cent of the mean amplitude at a stimulation frequency of 100 per second, which was the maximal value obtained in the circumstances of experiment. As it appears from Fig. 2 there is some justification for supposing that the relation between frequency and amplitude may be approximately exponential within the frequency range under consideration.

With the foregoing in mind the next step in analysis was undertaken with the result depicted in Fig. 3, which contains the results of three similar experiments upon the monosynaptic reflex pathways of triceps surae and upon those

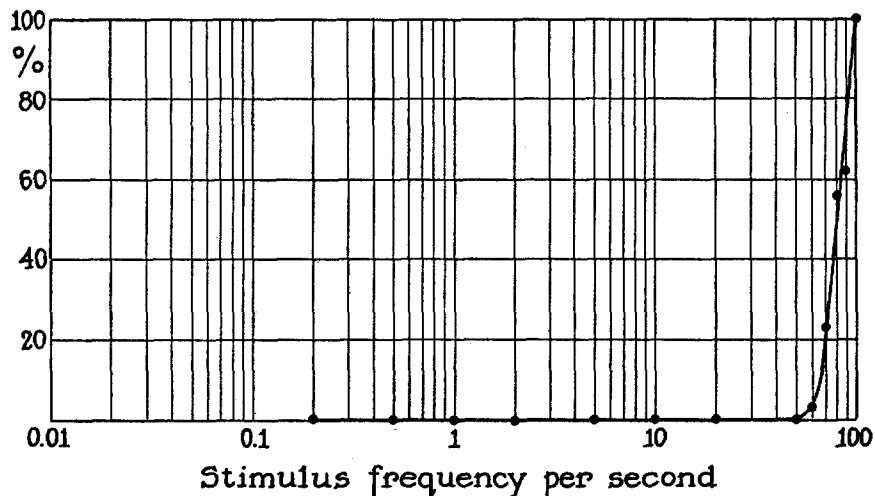


FIG. 2. Relation between frequency and mean monosynaptic reflex amplitude in the steady state. Low frequency response suppressed by nembital.

of flexor brevis digitorum. The manner in which Fig. 3 is constructed may require some comment. Values for mean monosynaptic reflex amplitude at the several frequencies, and in the several experiments, were plotted on semilogarithmic paper as a function of stimulus interval to find, by extrapolation to zero interval, the factors for scaling the values from individual experiments. The scaled values for monosynaptic reflex amplitude as given in Fig. 3 are represented on the ordinate in per cent of an arbitrary theoretical value for mean amplitude at zero interval, and on the abscissa according to interval between successive stimuli.

The curve plotted in Fig. 3 is the exponential decaying from the assumed arbitrary value at zero time to  $1/e$  in 4 msec. It is, therefore, the curve describing in approximation the decay of residual facilitation in monosynaptic reflex paths as originally determined in 1946 (6).

Now it is obvious that a number of secondary influences will come to bear

upon the realizable mean monosynaptic output as frequency increases from the range here employed toward infinity. However, and within the range, it is evident that the decay curve of residual facilitation is an adequate expression for the relation between frequency and mean monosynaptic reflex output *provided* that output is, or approximates, zero at frequencies in the neighbor-

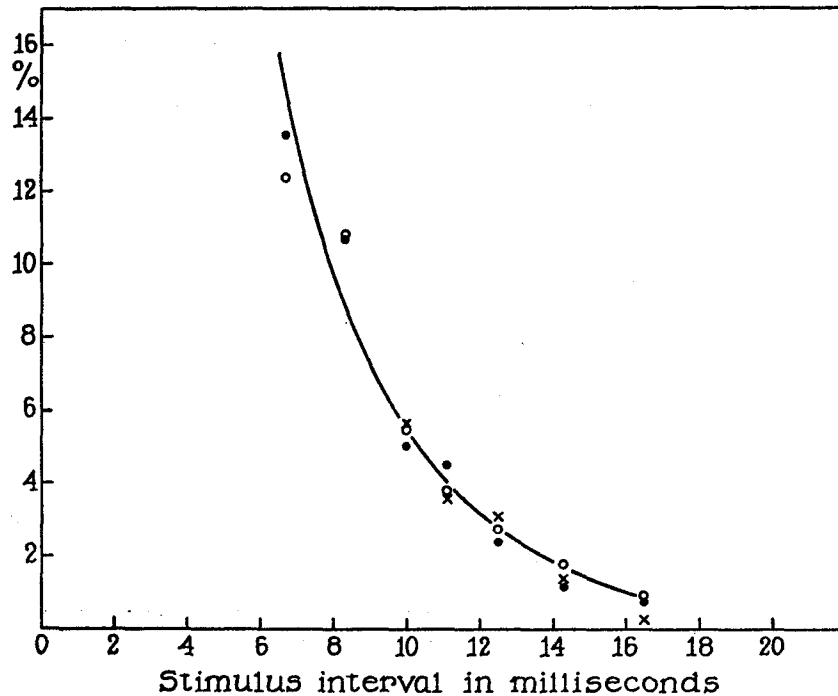


FIG. 3. Relation between frequency and mean monosynaptic reflex amplitude in the steady state plotted as a function of interval between successive stimuli. Results from three experiments scaled by extrapolating plots of log amplitude *vs.* stimulus interval to zero interval. Amplitude is expressed in per cent of an arbitrary value for amplitude at zero interval after scaling. The plotted curve is the exponential decaying from that arbitrary value at zero interval to  $1/e$  in 4 msec.

hood of 60 per second, this because residual facilitation decays to zero at conditioning shock-test shock intervals that are the approximate equivalent of that frequency. It will now be clear that the preparations were narcotized to the point of blocking low frequency monosynaptic reflex transmission in order to satisfy the proviso.

According to the present evidence there is sufficient reason for concluding that temporal summation in the rhythmically active monosynaptic reflex pathway is an expression of the same fundamental underlying process as is

residual facilitation, which latter, by the nature of its experimental demonstration (6) has the quality of spatial summation.

The reflex discharges here discussed constitute what Alvord and Fuortes call a "sustained reflex" (1). This being so, the situation raised by the present experiments is rather interesting, for Alvord and Fuortes have contrasted the anesthetized and decerebrate preparations with respect to sustained reflexes thusly: "anaesthetized preparations, though giving reflex reactions to single shocks—can only react with unsustained activity" and "in contrast to what has been found in anaesthetized animals the decerebrate cats examined, regardless of presence or absence of reflexes to single shocks, presented sustained reactions to repetitive stimulation." On the basis of the present experiments it would seem that the two sorts of preparation are not so very different from the standpoint of that which they reveal concerning the workings proper of the monosynaptic reflex pathways. That extraneous influences upon the monosynaptic reflex pathway are very different in the heavily narcotized preparation and the decerebrate preparation is obvious and granted, but such differences can only modify behavior of the anatomical pathway; they cannot be supposed to alter its fundamental intrinsic properties. In view of the differences in extraneous influence it is remarkable indeed that the external expression of monosynaptic reflex behavior is so little different in the two sorts of preparation.

The concept of the sustained reflex has been developed particularly in relation to heteronymous monosynaptic reflex transmission. Heteronymous transmission from one head of triceps to the other, for instance, is something that ordinarily does not occur with isolated or low frequency stimulation but does occur, as Alvord and Fuortes were the first to show, at frequencies above approximately 70 per second (1). Their finding has been amply confirmed during the present series of experiments and extended inasmuch as the high frequency heteronymous response has been found in decapitate and anesthetized preparations although possibly not in the same abundance as in decerebrate preparations.

Until recently it was not known that the heteronymous monosynaptic reflex connections of motoneurons by one means or another could be made to transmit short latency monosynaptic reflexes in response to single shocks. Prior to that discovery one possible, but not unique, interpretation of the facts was that a synaptic property possessed by homonymous connections, by means of which they secured short latency transmission, was lacking in heteronymous connections. Then, upon finding heteronymous transmission by temporal summation during high frequency stimulation, one might be led to suppose that different mechanisms are responsible for low frequency homonymous transmission and high frequency heteronymous transmission and further, by implication, that different mechanisms are responsible for low and high frequency homonymous transmission. This is, if not exactly, at least essentially, the concept of difference between the mechanisms of "unsustained" actions and "sustained" reflexes.

The finding of short latency heteronymous monosynaptic reflex response to single shocks in a variety of circumstances (*cf.* references 10, 12, and contained references) has removed any justification for supposing that other than quantitative differences characterize homonymous and heteronymous synaptic connections. This does not disprove different mechanisms for low and high frequency transmission. It does, however, remove a potential reason for postulating different mechanisms and, further, relieves one of the need for considering homonymous and heteronymous responses separately.

The present experiments substantiate the view that temporal summation in the monosynaptic reflex pathway depends upon operation of the "synaptic potential-residual facilitation mechanism." In doing so they show that temporal summation and sustained reflexes can be accounted for in terms of elementary processes that were discovered initially by the use of single volleys, and which are not peculiar to some particular type of experimental preparation.

Trains of stimuli sometimes have been employed in an attempt to mimic a naturally engendered reflex. Such an attempt can only be self-deceiving for the individual stimuli are synchronous equally with those employed in single shock stimulation, whereas the essence of the natural reflex, with few exceptions, is asynchrony of input. Nevertheless it is fair to ask in what manner asynchrony *per se* could be expected to alter the fundamental properties of synapsis. The essential problem presented by the fact of temporal summation is whether the "residual facilitation process" by summation comes to the point of engendering reflex discharge as is supposed in the concept of sustained reflexes, or whether it becomes merely a more intense facilitator of transmission.

Were the residual facilitation process to be shown capable by summation of engendering discharge in its own right, then, given an asynchronous input, one might argue that the brief synaptic actions documented by Hunt (4) would, by getting out of step, suffer a loss in efficacy that might conceivably parallel the supposed gain in efficacy of the residual process due to temporal summation. Were all this to happen one could then argue that the means of transmission, by reason of quantitative differences, is to some extent different in synchronously and asynchronously repetitive activity.

On the other hand were the residual facilitation process to remain a subliminal threshold lowering agency then, given again an asynchronous input, one might argue that the summation of this process changes threshold to a degree that compensates in some measure for the loss of efficacy suffered by reason of desynchronization of the brief transmitter actions.

By whichever means proposed the reflex product of asynchronous impingement, as in a stretch reflex, would be the same. In fact one cannot by means of present day methods come to any conclusion from observation of asynchronous activity as to the precise nature of the synaptic events responsible for discharge. Thus, while it is legitimate to synthesize the behavior of asynchronous activity making use of synaptic mechanisms demonstrated by the use of syn-

chronous activity, it is perhaps imprudent to deny the existence or importance of some synaptic event from observation of asynchronous activity.

The entire case for the belief that a long lasting synaptic action, now identified with the residual facilitation process, comes by temporal summation to the point of engendering discharge in its own right is built upon evidence obtained by the use of synchronous repetitive volleys rather than asynchronous input, and consists of the observation by Alvord and Fuortes (1) that response in certain circumstances may become randomized in time relative to the incoming afferent volleys. Since the circumstances include the use of extensor motoneurons in decerebrate preparations displaying extensor rigidity, there is ample basis for supposing that events extrinsic to the monosynaptic pathway proper are the essential cause of randomization when this occurs. But this is a problem discussed to greater advantage in connection with the study of response by individual motoneurons for which reason it is deferred until the behavior of individuals has been examined (9).

It must be understood that the present discussion concerning the probability that the residual facilitation process is essentially a threshold lowering agency rather than a transmitting agency need apply only to motoneurons. There is reasonable evidence in ever increasing abundance that some process of a relatively enduring quality, perhaps not unlike that under discussion, is responsible for high frequency repetitive firing in certain internuncial relays (*cf.* for instance reference 17). In this connection it might be well to promulgate the view that motoneurons constitute a rather special class of neurons functionally very important, of course, but numerically an insignificant part of the entire neuron population and not, perhaps, in their patterns of behavior representative of the usual. Surely as much might be said of the monosynaptic reflex pathways. Just as the reflex action served by these pathways is unique so, too, may be some aspects of the mechanism by means of which they perform the service.

#### SUMMARY

Monosynaptic reflex responses elicited by repetitive stimulation in the frequency range between 60 and 100 per second yield evidence of temporal summation.

The relation between stimulus interval and mean monosynaptic reflex response in the steady state at the frequencies studied is described adequately by an exponential decaying to  $1/e$  in 4 msec.

Since the temporal course of spatial summation is described adequately by the same exponential it is concluded that the two phenomena, temporal and spatial, are expressions of the same fundamental process intrinsic to the workings of the monosynaptic reflex pathway, to wit the synaptic potential-residual facilitation mechanism of prior descriptions.

Some discussion of implications is appended.

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