

TRANSMISSION IN FRACTIONATED MONOSYNAPTIC SPINAL REFLEX SYSTEMS

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The monosynaptic reflex systems of the spinal cord are divisible into units each of which concerns a group of muscles that act in reciprocal harmony at a given joint (9). Within each such "myotatic unit" may be found two fractions each internally linked in synergy by monosynaptic reflex excitatory interconnection: the two linked to each other in antagonism by inhibitory interconnection. With respect to monosynaptic reflex excitatory pathways the individual synergic fractions are the functional units. Anatomically a synergic unit may contain more than one muscle, as does the flexor synergic unit of the knee in which biceps femoris posterior and semitendinosus are the partners. The nerve supply of a synergic unit may be fractionated, frequently into natural bundles such as the two gastrocnemius nerves, medial and lateral, that together constitute the supply to triceps surae, the extensor synergic unit of the ankle. Once a synergic unit has been fractionated two sorts of monosynaptic reflex connection may be distinguished: those that afferent fibers of a given nerve bundle make with motoneurons of the same bundle, and those made with motoneurons of another bundle. For convenience the two sorts of connection may be described as *homonymous* and *heteronymous* respectively.

The influence of monosynaptic reflex afferent fibers is widely, probably completely, disseminated throughout the motoneuron pool of a synergic unit and cooperation of a number of such fibers is requisite for securing any monosynaptic reflex therefrom. Thus divergence and convergence of synaptic connection are extensive within the synergic unit. Nevertheless, monosynaptic reflexes elicitable within the synergic unit by stimulation of constituent fractions retain a high degree of the local sign or, more specifically, autochthony characteristic of response in the unfractionated unit (7, 8). This fact implies that the transmitter potentiality¹ of a given monosynaptic reflex

¹ For some purposes it is not sufficient to describe the degree of influence exerted upon a motoneuron by excitatory afferent terminations in terms of "intensity of action." For one or another reason the action may be highly effective from the stand-

afferent fiber with respect to the motoneurons supplied is related in some way to anatomical propinquity of receptor origin and effector termination within the muscle of the synergic unit. Difference in transmitter potentiality of a given monosynaptic reflex afferent fiber at its junctions with individual motoneurons of the synergic unit pool might be saltatory,² qualitative, and absolute (Fig. 1A), saltatory and facultative (Fig. 1B), or graded, quantitative, and facultative (Fig. 1C). By graded one can imply saltation in a number of steps.

The first mentioned possibility would imply that of all the endings supplied to motoneurons by a given afferent fiber those upon certain motoneurons possess some property necessary for transmitter action that is absent in the remainder. At the operational level this would mean absolute asymmetry of transmission in homonymous and heteronymous paths of the fractionated synergic unit and hence absolute autochthony, a necessary condition, incidentally, for ascribing unitary properties to the "ultimate myotatic unit" conceived by Fulton (3) to be comprised of a single muscle spindle and its surrounding fascicle of muscle fibers.

The second and third possibilities are consistent with a finding of heteronymous monosynaptic reflex discharge. Of these the second proposes in effect that the endings of a monosynaptic reflex afferent fiber are of two sorts with respect to transmitter potentiality, the distinction being either in quality or quantity. The notion may be said to arise in Cohen's (2) concept of distinct low and high threshold paths; one finely localized, the other diffuse; one providing "finesse and discreteness" of myotatic adjustment, the other strength in violent movement; the transition, or reflex irradiation, being abrupt and steplike. It is the last of the possibilities, however, that receives a measure of support from the observations that follow. It proposes that the connections an afferent fiber establishes with motoneurons of the synergic unit vary widely, but only quantitatively, with respect to transmitter potentiality. The observations to be described were made initially in a search for heteronymous monosynaptic reflex transmission and subsequently in an attempt to explore the factors governing its appearance.

point of securing postsynaptic response, but relatively ineffective in facilitating the action of a convergent path. The converse likewise may hold. Introduction of the terms "transmitter potentiality" and "facilitator potentiality" fills the need for means of describing aspects of presynaptic action that are not necessarily covariant. These terms can be employed without prejudice as to mechanism. The present study is concerned only with transmitter potentialities and the arbitrary numerical values assigned in Fig. 1 to exemplify the propositions should not be thought to have any relation to facilitator potentialities.

² Implying a "sudden and abrupt change" rather than an "advance by leaps and bounds."

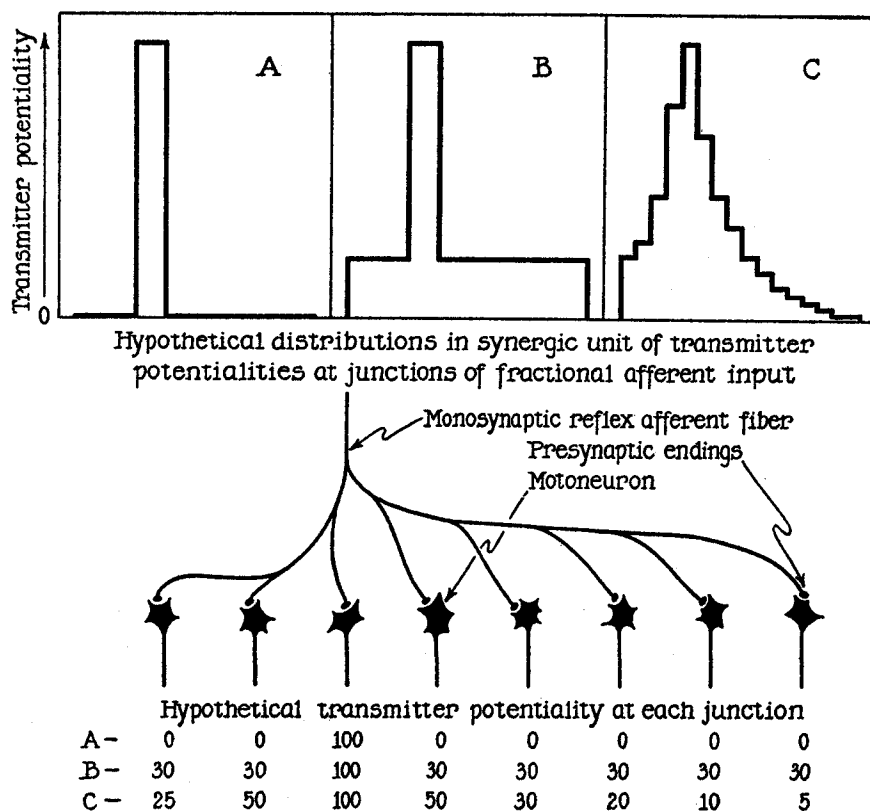


FIG. 1. Diagrammatic representations of three hypotheses (A, B, C) concerning the manner in which the transmitter potentiality of a given monosynaptic reflex afferent fiber might vary in its distribution throughout the motoneuron population of a synergic unit. In the lower part of the figure the motor pool of the synergic unit is represented in eight fractions by as many motoneurons. The afferent inflow from a fraction of the units is represented by a monosynaptic reflex afferent fiber that distributes presynaptic endings throughout the pool. Each ending represents *not* a single synaptic knob but the sum total of synaptic knobs constituting the junction. Below each motoneuron in columns are arbitrarily assigned numerical values to represent, according to the three hypotheses, the transmitter potentialities of the several junctions. The distribution of transmitter potentialities throughout the pool from the afferent inflow of some other fraction of the unit would be different.

Considerable attention recently has been devoted to evidences of heteronymous reflex transmission in fractionated monosynaptic reflex paths (1, 2, 4, 5, 6, 12). In most instances a background of decerebrate rigidity or frank induction of homonymous activity, as by muscle stretch, has been an ingredient of the experimental situations. In all such instances it need not

be supposed that the heteronymous connections played other than a facilitative role. However, Granit and Ström (4) encountered a single motoneuron out of presumably a large number that responded, without the need for stretch-evoked homonymous background, to either of two synergic nerves. If, as appears to have been the case, the homonymous nerve was intact then resting spindle discharge from homonymous muscle might have supported the heteronymous discharge. On the other hand Job (6) reports the spread of monosynaptic reflex activity from one to the other gastrocnemius nerve during and especially 2 minutes after tetanization.

Decapitate preparations have been employed, additional operative procedure being limited to exposure within a paraffin pool of chosen pairs of synergic nerves: these included in one or another experiment the two gastroc-

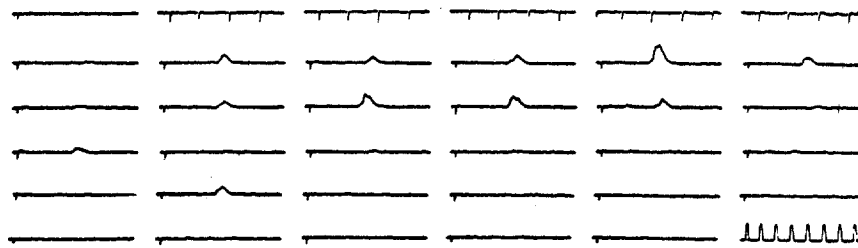


FIG. 2. Heteronymous monosynaptic reflex transmission from medial gastrocnemius afferent fibers to lateral gastrocnemius motor fibers following tetanization of the afferent pathway. Records made every 2 seconds before, during (top row), and following (second and subsequent rows) a 10 second tetanus at *ca.* 500 per second. Time at bottom right in milliseconds. Temperature, 39.5°C.

nemius nerves, those of flexor longus, of the flexor hamstrings, semimembranosus, the ankle flexors, and divisions of the plantaris nerve. Of each synergic pair one was fitted with electrodes for stimulating, the other with electrodes for recording. Since the spinal cord was not exposed rectal temperature was a reasonable indicator of spinal cord temperature. The search for heteronymous transmission was made in the resting state at normal temperature, at lowered temperature, and during periods of post-tetanic potentiation (10) in which periods effectiveness of presynaptic volleys is greatly enhanced. A most important point of technique is to secure afferent silence in the homonymous pathway to the motoneurons undergoing observation for heteronymous response: it must necessarily be severed, free from injury discharges and, above all, not inadvertently stimulated.

Standard experimental procedure has been to stimulate rhythmically at low frequency (25 or 30 per minute) and to interpolate, when desired, a 10 second period of high frequency stimulation (approximately 500 per second). The low frequency stimuli were sweep synchronized, each sweep for an

interval prior to, during, and following high frequency tetanization being photographed.

Fig. 2 illustrates an experiment in which the monosynaptic pathways of gastrocnemius muscle were examined for heteronymous transmission, the nerve to gastrocnemius medialis serving as the afferent limb, that of gastrocnemius lateralis and soleus as the motor limb, of the heteronymous path. The recordings are arranged to read in book-wise order, five lines, or 30 recordings, representing 1 minute elapsed time. During the initial 40 seconds following tetanization small heteronymous monosynaptic responses may be

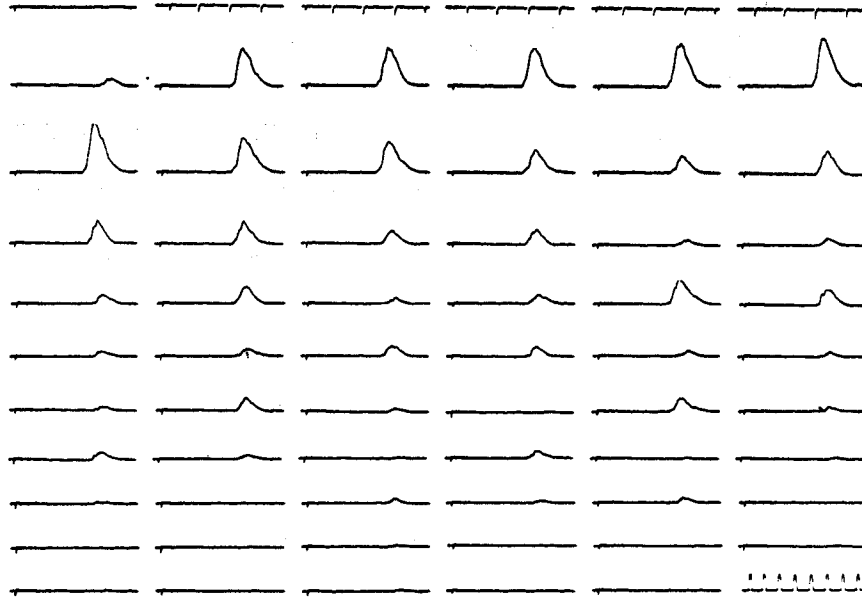


FIG. 3. As Fig. 2 from same preparation. Temperature, 33°C. Note increased latency and spike potential duration.

found. In similar circumstances of stimulation potentiation of response in homonymous paths would endure for 3 or more minutes.

Lowering of body temperature is a means for increasing the intensity of heteronymous transmission and for prolonging the post-tetanic period during which it may occur. The observations of Fig. 2 were made at a time when rectal temperature was 39.5°C. Upon lowering temperature to 33.0°C. post-tetanic heteronymous transmission again was tested with the result illustrated in Fig. 3. In the changed circumstance heteronymous monosynaptic reflex transmission was augmented and responses could be obtained well into the 2nd minute following cessation of the conditioning high frequency tetanus. In several experiments, body temperature being between 32.0°C. and 32.5°C.,

heteronymous monosynaptic reflex transmission could be obtained in the 3rd minute after tetanization, and in one instance, at 32.0°C., a small reflex occasionally appeared without the aid of prior tetanization or other recognizable supportive activity. Asphyxiation at a critical stage can precipitate the occurrence of heteronymous monosynaptic reflex transmission.

The experiment illustrated by Fig. 4 presents an example of heteronymous monosynaptic reflex transmission in flexor hamstring pathways, nerves of biceps femoris posterior having been stimulated, response of semitendinosus motoneurons having been recorded. Body temperature at the time of recording was 38.0°C.

The preparation contributing the result in Fig. 4 was of considerable interest for it twitched vigorously after lowering body temperature to 33.5°C. With

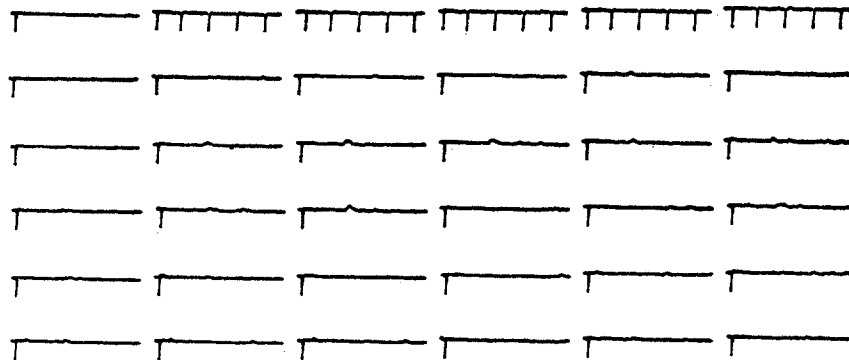


FIG. 4. Heteronymous monosynaptic reflex transmission from biceps femoris posterior afferent fibers to semitendinosus motor fibers. Temperature, 38.0°C. All other details as in Fig. 2.

the activity engendered by constant twitching of the trunk and forelegs as background, small discharges appeared in the semitendinosus nerve without the aid of prior tetanization (Fig. 5). Many of these appeared in appropriate short latency monosynaptic reflex time with respect to stimulations of biceps femoris posterior nerve and presumably were aided if not secured by the afferent volleys resulting therefrom.

The observations presented, and those of others (1, 4, 6, 12) bearing on the same theme, do not constitute a definitive demonstration that heteronymous connections possess intrinsic transmitter potentiality, for that would require the finding of heteronymous transmission in the absence of all convergent excitatory activity, a requirement not likely to be met. Nevertheless, the grounds for supposing heteronymous connections incapable of transmitting have been shrunken considerably, to the point in fact that one may suppose, with but minor reservations, that the autochthonous character of fractional

monosynaptic reflexes is not absolute and that the properties of individual excitatory synaptic endings of the monosynaptic afferent fibers upon some motoneurons need not be fundamentally dissimilar to those endings upon some other motoneurons. In brief, the proposition depicted in Fig. 1A is effectively, if not definitively, excluded.

If, now, it be granted in accord with either of the propositions depicted in Fig. 1, B and C that all monosynaptic excitatory connections possess some degree of transmitter potentiality then by dichotomous fractionation of the entire innervation of the synergic unit two bundles of monosynaptic afferent fibers are obtained each of which possesses for its homonymous motoneurons a high average transmitter potentiality per afferent fiber and for its heteronymous motoneurons a low average transmitter potentiality per afferent fiber (7, 8, 4, and the present results). Upon further dichotomous fractiona-

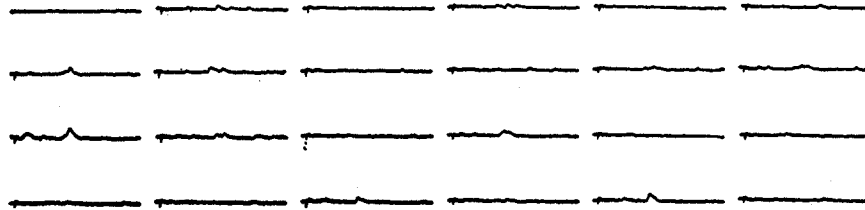


FIG. 5. From same preparation as Fig. 4. Temperature, 33.5°C. No tetanization. Preparation twitching spontaneously. Convergence of "spontaneous" activity and biceps femoris posterior afferent volleys resulted in monosynaptically timed discharges in semitendinosus nerve.

tion to yield four bundles one would expect to find each bundle possessing for its homonymous motoneurons a higher average transmitter potentiality per contained monosynaptic afferent fiber than it does for the heteronymous motoneurons in each of the three remaining fractions. However, if the converse relations be considered then according to the notion depicted in Fig. 1B the average transmitter potentiality upon the motoneurons of one fraction possessed by each of the remaining three fractions should be approximately equal per contained monosynaptic afferent fiber. On the contrary, if transmitter potentiality is graded according to the representation in Fig. 1C then the average transmitter potentiality of each of those remaining fractions should be unequal per contained monosynaptic afferent fiber.

In order to devise a practical test for equality or inequality of heteronymous bundles two facts must be considered: that monosynaptic reflex transmission displays a central threshold and that synaptic efficacy of convergent reflex paths is not merely additive. Together these facts will ensure that fractionation by successive dichotomies must at an early stage result in bundles of monosynaptic afferent fibers none of which would be capable of provoking

discharge in any of the fractional motoneuron pools. This difficulty can be circumvented by practicing asymmetric fractionation in such a way that attenuation of transmitter potentialities is minimized. For instance, one small bundle can be reserved as a motor limb for recording such heteronymous reflex discharge as may occur, and the remaining, much larger, fraction of the innervation divided into two bundles the heteronymous transmitter potentialities of which may be compared.

Fig. 6 contains observations from an experiment in which the nerve to lateral gastrocnemius and the larger of two fractions of the nerve to medial

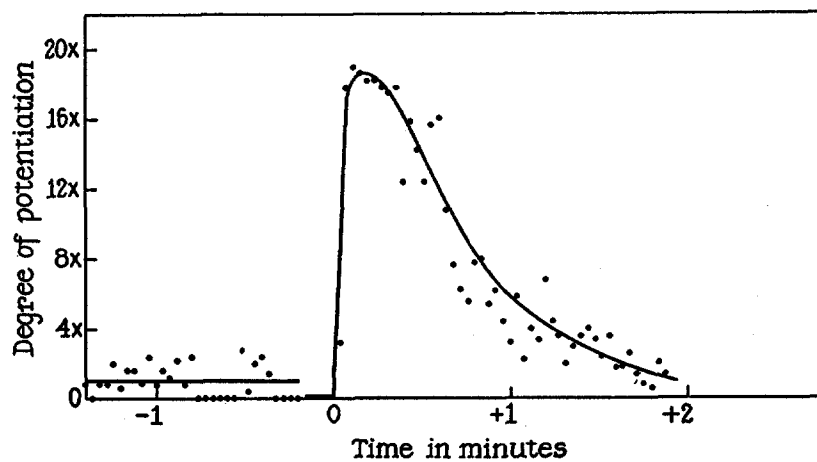


FIG. 6. Monosynaptic reflex discharges resulting in a small twig of medial gastrocnemius nerve from stimulations of the larger remainder of medial gastrocnemius nerve before and after 12 second tetanization of the afferent path. Ordinates, amplitude of monosynaptic responses expressed in multiples of average pretetanic value. Abscissae, time in minutes relative to end of tetanization.

gastrocnemius served as afferent channels, the smaller of those two fractions as motor path. In this experiment stimulation of the entire lateral gastrocnemius nerve, even at the peak of its potentiated action was incapable of securing monosynaptic reflex discharge in the recorded bundle. The responses plotted in Fig. 6 are those obtained by stimulation of the larger medial gastrocnemius fraction at 25 per minute prior to and following a 12 second high frequency tetanus. Zero time is fixed at the close of tetanic stimulation. Amplitude of response in arbitrary units is plotted on the ordinates and is expressed in multiples of the average resting amplitude.

In the resting state prior to tetanization heteronymous transmission from the larger to the smaller fraction of medial gastrocnemius nerve although small in amount, and irregular, was present. The result demonstrates that

anatomical asymmetry can be made to compensate for functional asymmetry and, the compensation achieved, that functionally drastic measures need not be employed to secure heteronymous transmission in the absence of homonymous background. At the peak of potentiation response was increased 19-fold from average resting value. In duration the period of potentiation greatly exceeded that encountered in heteronymous pathways between natural heads of a muscle (Figs. 2 and 4) except when the latter are chilled (Fig. 3).

Thus, it can be said that the heteronymous transmitter drive by somewhat less than the total medial gastrocnemius monosynaptic afferent fibers upon the motoneuron pool of the remainder in terms of reflex efficacy was in fact far greater than the heteronymous drive by the entire lateral gastrocnemius monosynaptic inflow. In other words heteronymous connections per fiber from different sources need not be equal with respect to transmitter potentiality, which fact is in favor of the concept of grading as depicted in Fig. 1C, although the fineness of grading is not thereby revealed.

Experimental support for either of the propositions depicted in Fig. 1A and 1B would have provided some basis for ascribing functional significance (*cf.* references 2 and 3) to the distinction between homonymous and heteronymous pathways. As it would now appear the distinction, notwithstanding its utility for many analytical purposes, is purely artificial.

COMMENT

The fact that monosynaptic reflex transmission in a fractionated system is not in all circumstances reliably autochthonous has a potentially important consequence, since most experiments involving monosynaptic reflexes rely upon the recording of responses in severed ventral roots, the fiber content of which is not limited by anatomy to the unit or fraction of a unit stimulated. Whenever, in such experiments the entire monosynaptic afferent fiber input of the synergic unit is stimulated then the monosynaptic reflex output within the severed ventral root certainly pertains to the motoneuron pool of that unit (7). Further, if a fraction of the input (say medial gastrocnemius) is stimulated it would still be correct to refer the reflex output in the ventral root to discharge from the motoneuron pool of the unit (*i.e.* triceps surae), but in some circumstances it would not be correct to refer the reflex output to the specific fraction of the motoneuron pool (*viz.* medial gastrocnemius). Post-tetanic potentiation is one such circumstance (*cf.* reference 5, Fig. 11). The importance of respecting the limitation lies in the fact that as yet unsuspected conditions for breakdown of rigid autochthony in the fractional monosynaptic systems may exist. Even so, the error involved, on present evidence, would not be great. In the study of individual motoneurons responding to monosynaptic afferent reflex volleys identification of the motoneurons with one or another fraction of the pool usually is a simple matter (11).

No plausible reason now exists for equating transmitter potentiality of a monosynaptic reflex afferent fiber at one or another of its junctions to motoneurons with the possession by some of its endings of a functional property denied to others. One looks then to structural and organizational variables with which transmitter potentiality may vary. The more obvious of these are size, numbers, and aggregation of the endings by which any given monosynaptic reflex afferent fiber is joined to any given motoneuron of the synergic unit. It might be justifiable to regard size variation as the equivalent of numerical variation of endings in the highest state of aggregation, and by so doing perhaps to reduce the number of variables that must be considered when attempting to account for the character of monosynaptic reflex transmission. Since the present observations do not contribute toward an understanding of the relative significance of the proposed presynaptic variables as quantitative determinants of transmitter potentiality the discussion of them is interrupted at this point.

SUMMARY

A study has been made of conditions that support monosynaptic reflex transmission from afferent fibers of one part of a synergic muscle mass to motoneurons of another part. Heteronymous response so called can be brought on by prior tetanization of the afferent pathway and by asphyxiation to a critical stage. The response is facilitated by cooling and may appear in the cold preparation without need for prior tetanization.

By appropriate asymmetrical subdivision of a monosynaptic reflex system an afferent inflow can be obtained that is sufficiently powerful to secure heteronymous transmission without the need for prior tetanization or cooling.

Each junction between a monosynaptic afferent fiber and a motoneuron possesses some degree of potentiality for transmitting. Transmitter potentiality of an afferent fiber at its several junctions with motoneurons varies widely. Reasons are advanced for supposing the variation to be graded rather than stepwise, and quantitative rather than qualitative.

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