

ELECTROMYOGRAPHIC AND MONOSYNAPTIC DEFINITION OF REFLEX EXCITABILITY DURING MUSCLE STRETCH

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MONOSYNAPTIC testing of motoneurone excitability was introduced by Renshaw (23). It has become an important tool in reflexology, particularly after Lloyd's (16) demonstration of a significant monosynaptic component in stretch reflexes. In this laboratory we have been interested in applying the method to natural stimuli and developing it for use with single ventral horn cells (7, 8, 9, 10). Recent resourceful experimentation by Magladery and his collaborators (18, 19, 22) has expanded the applicability of monosynaptic testing to man as initiated by Hoffmann and his group (12, 25, 26). An important methodological study with single conditioning and test shocks has been completed by Brock, Eccles and Rall (2), particularly from the point of view of electrical thresholds of muscle afferents.

In this paper we compare monosynaptic testing with electromyography. Stretch is applied to the gastrocnemius muscle and to part of a ventral root taken out for monosynaptic testing while the rest of the ventral root supply is intact and delivering reflex stretch impulses which are picked up by electromyography. (In our previous contributions all ventral roots from L5 downwards were severed.)

The monosynaptic test has in the past been used in two ways. (i) Conditioning and test shock on the same nerve. This has recently been called *homosynaptic* testing. (ii) Conditioning and test shock on synergists such as, in our case, the medial and lateral gastrocnemius nerves, so called *heterosynaptic* testing. These terms, introduced by Eccles and his collaborators (2), are convenient in describing experiments but not strictly adequate. "Homosynaptic" suggests identical fibres (synapses) for conditioning and testing. However, when conditioning is done by stretch, it is hardly probable that the monosynaptic component used for testing the motoneurons is the only one engaged. There is polysynaptic facilitation from muscle nerves (11), particularly probable in stretch (22), and we have no theoretical reasons for assuming that all facilitatory stretch afferents are monosynaptically connected (6, 17, 22).

Problem and principle of analysis

The experiments to follow will serve to investigate some implications of a general thesis suggested by the work of Granit and Ström (9) on single ventral horn cells. During stretch the size of the monosynaptic test volley,

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recorded from the severed ventral root, increases above its original control value for the resting muscle (7, 16). The initial phase of this increase is indicated in the scheme of Figure 1. The rise of the test curve signifies recruitment of fresh neurones from the fringe. The test curve therefore shows that there has been enough conditioning by stretch afferents to make a synchronous test volley capable of traversing the neurones activated. It measures the total number of active and fringe neurones but gives no information as to the degree of activation beyond stating that their level of excitability is sufficient for the transmission of a synchronous test shock. Electromyography, however, is here a "discharge test." During slow stretch motoneurons

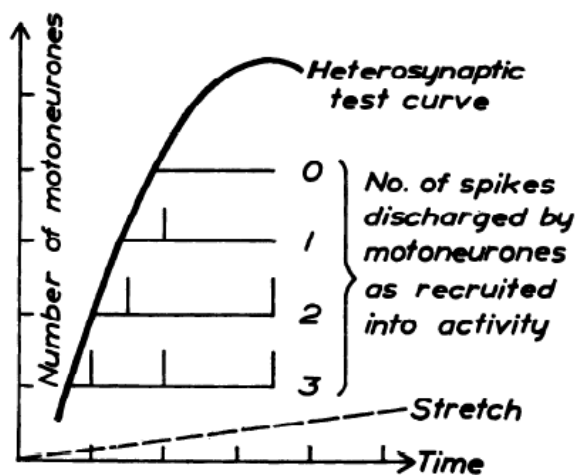


FIG. 1. Diagram illustrating facilitation during stretch indicated by heterosynaptic test curve, and discharge of selected motoneurons. (See text.)

may discharge once, several times, or not at all. It is likely that the neurones in the active zone discharge several times while those in the fringe zone do not discharge at all although they are capable of transmitting a monosynaptic test shock (9). This is illustrated in the diagram of Figure 1 by the spikes indicated at different levels of the monosynaptic curve which measures the rise of facilitation during stretch. The diagram raises the question as to whether during stretch the average reflex effect can without exception be assumed to be correctly gauged by a fringe test, *i.e.*, by the ordinates of a curve such as the one plotted. This question is not only of methodological interest. If the "transmission test" (monosynaptic testing) and the "discharge test" (electromyography) are very much at variance this also involves the definitions of "excitation" and "inhibition."

METHODS

Figure 2 presents the arrangement of the preparation for monosynaptic recording. Decerebrate cats were used in order to have active spinal cords and extensors prone to discharge. Both legs were denervated and the ileopsoas muscles cut across. For the experiment, however, there remained the medial and lateral nerves of the gastrocnemius-soleus muscle which itself was attached to the Brown-Shuster myograph pulled on by the stretch device (7). Figure 3 shows the slow stretch applied, at low sensitivity of the stretch recording system, together with a series of electromyograms of stretch reflexes taken in succession from the same place in the belly of the gastrocnemius-soleus muscles. The electrodes were silver or platinum pins, around 3 cm. in length. They were stuck in obliquely through the upper fleshy portion of the gastrocnemius well down into the soleus. Generally several places were tried but often it happened that a particular place showed great activity and then the electrodes were left in this position.

From a half to about a quarter or somewhat less of the L7 or S1 ventral root was isolated and cut across to be placed on the electrodes for recording the monosynaptic volley (Fig. 2) from the gastrocnemius nerves. Sometimes L6 and the ventral roots below S1 were severed before the experiment.

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The monosynaptic test shock was placed in different temporal positions during stretch, each position tested 5–8 times, and the values averaged. Electromyograms were taken before, during, and after a run of monosynaptic testing. The temporal loci within which discharges occurred in the muscle were marked off and, in addition, the loci of any visible impulses in the ventral root filaments from which the monosynaptic response was recorded. Together, these two records showed when firing occurred. Spontaneous discharges were checked up. Naturally the method can hardly be said to be quantitative with regard to the total amount of reflex firing into muscle and test filaments—in the latter there were mostly synchronized groups—but it gave a good indication of whether there was much or little firing and how discharge periods were placed relative to the curve traced by the monosynaptic indicator.

Sources of error. There is first a methodological error in the representation of the pool by one fifth to one half of one root. The same error occurs in the work of Magladery and

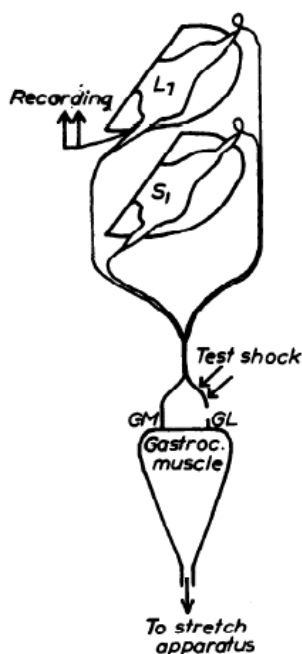


FIG. 2. Diagram of arrangement for recording by the heterosynaptic technique monosynaptic response from part of the root while the rest of it delivers impulses to the muscle during stretch.

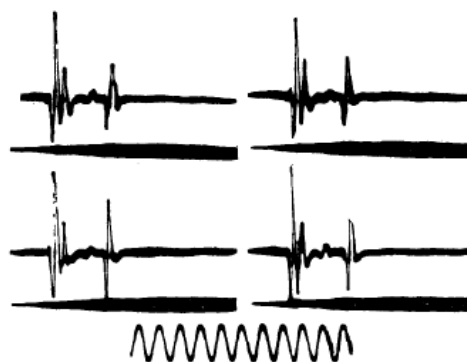


FIG. 3. Electromyograms during stretch taken from four sweeps. Below each record of spikes myograph record of stretch, at low sensitivity to prevent overloading amplifier. Time 100 c./sec.

his collaborators (18, 19, 22) with intrathecal recording of the monosynaptic response in man from filaments which the internal electrode happens to touch. This error is part of the methodological problem and will be discussed in the light of the experiments. Through the intact part of the root there will be restimulation of the pool from the loop represented by the external circuit through the muscle sense organs, causing what used to be called the "tonic" or "myotatic" appendage (3). This means a secondary shower of impulses beginning, at the earliest, some 5 msec. after the initial afferent volley has excited the centre to discharge. This effect may be more prominent in the intact motoneurons than in those isolated by root section. It should, however, be reflected by the heterosynaptic method of testing (see below, Discussion) which is nothing but synergist testing by sampling.

The size of the monosynaptic control must not vary significantly when two test curves are compared from the same muscle at *e.g.* different degrees of initial tension. Attention has been paid to this factor and we have selected for comparison only such experiments within which the monosynaptic controls have been practically equal. As the control normally increases somewhat in the course of an experiment we have kept stretch running at the usual interval of 5 sec. for half an hour or more before beginning to record the results. In the last experiment (Fig. 8) a variation took place as a consequence of the experimental

procedure (comparison before and after spinalization) but in this case we have given the absolute values.

Homosynaptic testing measures average refractoriness and subnormality in that portion of the root (to be called the test filaments) which is on the recording electrodes. Thus great variations of the test response can occur depending upon whether the natural volley, caused by stretch, happens to turn up just before or just after a test shock in a given position. This variation, unless recognized, may lead to false comparisons with the electromyographic test. Homosynaptic testing is further complicated by peripheral or afferent depression of the test volley, caused by refractoriness succeeding the natural stretch impulses, a factor which is negligible at light initial tension but can be serious at high initial tension with a heavy afferent discharge. Homosynaptic testing, on the whole, is to be used with caution and conclusions derived from it confirmed with other methods. In this respect we are in full agreement with Eccles and his collaborators (2), and in all work from this laboratory both methods have been employed in parallel (7, 8, 9).

Our stretching device is not quite free from mechanical vibration (a better one being under construction) but this should not be a serious error when two methods are compared under similar circumstances.

RESULTS

Each of the five experiments selected for illustrating the results represents a situation that must be described and analyzed as an entity.

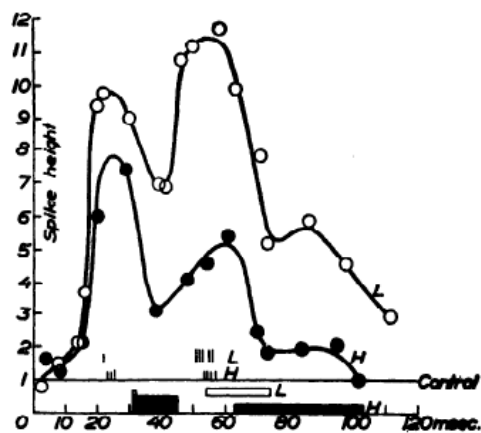


FIG. 4. Monosynaptic response during stretch at light (L) and high (H) initial tension. Black (H) and white (L) oblongs illustrate muscle discharge and corresponding spikes (H) and (L) above control line mark discharge in test filaments. Full explanation in text.

seen in the test filaments at the two states of tension. Below the line are found the corresponding discharge times obtained electromyographically, higher oblongs representing greater total activity. The electromyograms generally varied in size and temporal location but a large number of records has been considered in drawing the oblongs. Ventral root discharges will be, on an average, around 2 msec. in advance of what would have been their electromyograms if the roots had been intact. There is no correction for this interval in the diagrams.

Considering, to begin with, both curves together, it is evident that in both cases there is dominant facilitation since all the values are above the

EXPERIMENT 1. This is a comparison of light (L) and high (H) initial tension for 3 mm. stretch. The monosynaptic control is represented by ordinate 1.0 in Figure 4. The average controls in the two states of initial tension did not differ by more than 1:1.15 (see previous section). The test shock was placed on the intact medial gastrocnemius nerve and thus, with respect to it, was homosynaptic whilst heterosynaptic with respect to the similarly intact lateral component. As much as half of the ventral S1 was used for the recording of the monosynaptic test response. (There are generally more active neurones in S1 and a greater number of non-firing fringe neurones in L7.)

Above the control line are marked in correct relative size and number the synchronized spike groups (stretch reflexes)

level of the control. There is less facilitation, by this index, at the higher tension. The drop in the level of facilitation from L to H is due either to (i) motoneurone depressions, by which is meant the refractoriness and subnormal excitability which succeed an impulse, to (ii) true autogenetic inhibition (2, 4, 7, 8, 9), to (iii) a diminution of afferent inflow (5, 20, 21) or to all these factors. It is difficult to ascribe a significant effect on the general level of the curves to (iii), a diminution of afferent inflow. There are more muscle spikes at the higher tension which also, as such, should favor afferent excitation (14, 20).

Light initial tension. In curve L the single initial volley in the recording test filaments gave definite refractoriness for the test shock when alternated with it. This volley would therefore be followed by removal of active motoneurons, and the drop found in the monosynaptic response curve is to be expected for this reason alone. The placing of the test shock on either side of a "natural" volley is a good test for motoneurone depressions. When this test was applied later on, in the second discharge period of the test filaments, the monosynaptic response was found to traverse it without being in the least suppressed after firing. On the contrary, the curve rose and the simultaneous electromyogram suggests that the rise actually belonged to the muscle tested. We could, of course, assume that the greater part of the secondary discharge period belonged to the heterosynaptically tested lateral component of gastrocnemius but would not be forced to accept this conclusion. Also with pure homosynaptic testing the secondary discharge period shows less of the phenomena of depression (see below Exp. 2) than the first.

High initial tension. In this case we have still more reason to ascribe the early drop in the test curve to motoneurone depressions after the early discharge in the test filaments which in this case is heavier, also in the muscle, but at the higher initial tension a greater number of inhibitory afferents must also have been mobilized (7, 8, 9). Therefore we cannot exclude the fact that the greater depression of the general level of the curve might also in some measure be due to true autogenetic inhibition. This inhibition would be concealed (7) because the curve as a whole runs above the control line. It would explain why the secondary discharges in the test filaments for curve H are smaller than those for curve L. The sum total of muscular and filament spike activity, however, is greater for curve H than for curve L although the monosynaptic curve indicates diminished number of motoneurons. In this sense the two tests are at variance as indicators of average reflex excitability.

EXPERIMENT 2. This is a comparison of homosynaptic with heterosynaptic testing for 2 mm. stretch at high initial tension, the records (Fig. 5) being from a quarter of L7 in an animal in which only the medial gastrocnemius nerve was intact. This nerve was used for the homosynaptic and the lateral component for the heterosynaptic test because it so happened that in this animal the two monosynaptic controls, despite their difference of origin, were of the same size. Stretch began at the vertical line and im-

mediately elicited a large synchronous spike in the test filaments with consequent homosynaptic motoneurone depression. The drop of the curve so far below the control line suggests that there also could have been some diminution of the test spike on the afferent side. The afferent side was not tested in this particular case but in other similar experiments an initial drop of the homosynaptic curve was found to occur when the test spike had diminished

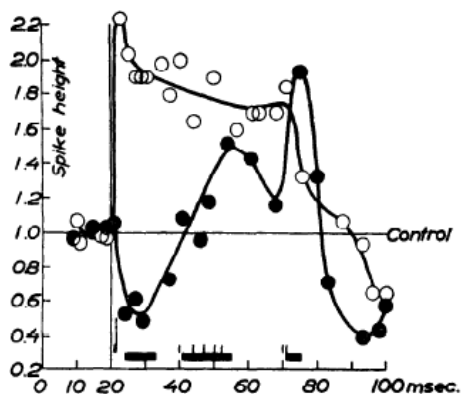


FIG. 5. Homosynaptic (filled circles) and heterosynaptic (circles) test curves for stretch at high initial tension. Full explanation in text.

on the afferent side. This notion is supported by the fact that at the minimum of the curve there was considerable firing into the muscle and simultaneously general facilitation indicated by the heterosynaptic test.

Firing was resumed in the test filaments when the curve reached the control line, and again the secondary as well as the third discharge period failed to be accompanied by homosynaptic depression.

It should be emphasized that *in no case have we seen any firing in the test filaments when the homo- or heterosynaptic curve has been below the control line.* An exception is, of course, afferent refractoriness which influences the test curve by diminishing the testing volley. But otherwise any given amount of firing in the test filaments is compatible with all levels of the test curves from practically 1.0 upwards.

The homosynaptic curve of Figure 5 brings further evidence for the conclusion that secondary discharge periods differ from the first one in that they can be accompanied by a rise instead of by a fall of the homosynaptic curve.

The heterosynaptic curve showed permanent facilitation gradually turning into inhibition below the control line at around 90 msec. Since high tension was used, there must have been true autogenetic inhibition earlier in stretch than that. The activity in the muscle suggests that the afferent inflow was quite good throughout stretch. For further information it was necessary to repeat heterosynaptic testing at lower initial tension of the muscle. This is done in the next experiment.

EXPERIMENT 3. The new curve (open circles) at light initial tension is compared with the foregoing one (filled circles) in Figure 6. It obviously lies above the curve obtained at higher initial tension. There is no reason whatever to assume that the muscle receptors were more active at the lower initial tension. On the contrary, there was only a scanty and late discharge in the test filaments and, at about the same time, some firing into the muscle, small compared with the activity at the higher initial tension. Therefore it is difficult to ascribe the slow drop in the heterosynaptic curve at high tension to cessation or diminution of the afferent discharge (20, 21). There must be some process capable of removing fringe neurones without

being able to prevent greater activation of the active zone of the total pool. The lighter tension raised a large fringe capable of transmitting the test shock but very few of these neurones could support a true reflex effect.

EXPERIMENT 4. This was an animal in which the efferent supply was curtailed because one third of both L7 and S1 were severed from the beginning to serve for the recording of the monosynaptic test volley. Both gastrocnemius nerves were, to begin with, intact. The muscle was at relatively high initial tension and testing was begun partly homosynaptically with the test electrodes on the medial gastrocnemius nerve. There were three small

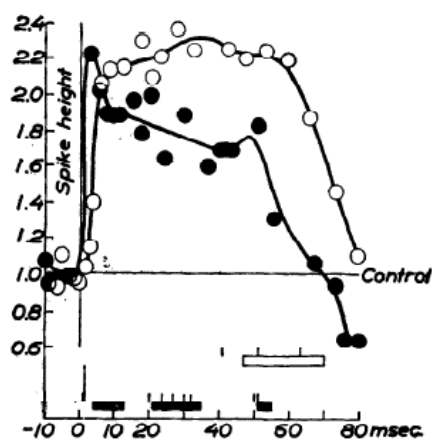


FIG. 6. The heterosynaptic test curve (filled circles) from Fig. 5 compared with same after decrease of initial tension of muscle. Full explanation in text.

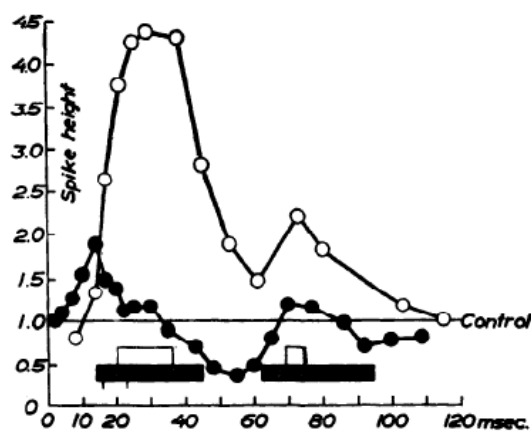


FIG. 7. Heterosynaptic (circles) compared with homo-heterosynaptic (filled circles) test curve during stretch at high initial tension. Full explanation in text.

spikes in the test filaments of L7, used for the lower curve (filled circles of Fig. 7). It was one of the common cases in which the reflex discharge in the test filaments was seen chiefly in the S1 filaments. The black oblongs show a great deal of firing into the muscle. As soon as this began the curve turned downwards as if there actually had been a really vigorous discharge in the test filaments.

The medial gastrocnemius nerve with the test electrodes inserted was cut and the heterosynaptic curve recorded (open circles). This time there were no spikes in the test filaments. Since a drop in this curve coincided with the fall of the (partly) homosynaptic curve below the control line and since tension was relatively high, one would again have to expect some concealed autogenetic inhibition. Diminution of impulse activity owing to severance of one nerve makes strict comparison difficult. The test with the S1 filaments could not contribute much to the elucidation of this case. It showed a somewhat greater and more prolonged drop below the control line than the test curve for L7 but there was a great deal of firing in the test filaments and so motoneurone depression would have had to be taken into account. In both homo- and heterosynaptic testing the secondary discharge period differed from the first in that it coincided with a rise instead of with a fall of the curve.

EXPERIMENT 5. This has been selected from a case in which the animal was spinalized at the upper lumbar level in the midst of an experiment. The ordinates of Figure 8 are in microvolts. It was heterosynaptic testing with about one fifth of the ventral root L7 on the recording electrodes. The monosynaptic control, though regular, was unusually small, only $15 \mu\text{V}$. The electromyographic response (black oblong) was very late. There were no impulses in the test filaments. The good facilitation observed in the curve (filled circles) was apparently a fringe phenomenon. Spinalization abolished the monosynaptic control response altogether. It was still absent, when, 20 min. later, the second curve (open circles) was obtained but a very small facilitated response turned up in the region coinciding with the electromyogram (white oblong). The latter was practically as much in evidence as

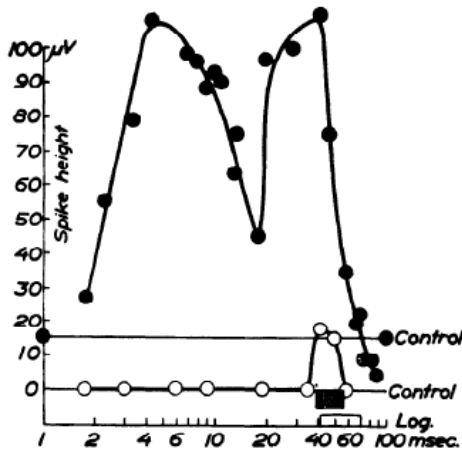


FIG. 8. Ordinates in absolute measures. Otherwise as Fig. 4. Heterosynaptic facilitation tested by means of severed lateral gastrocnemius nerve during stretch before (filled circles) and after (circles) spinalization as explained in text.

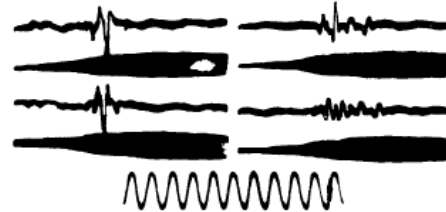


FIG. 9. Electromyograms from experiment illustrated in Fig. 8. On left, before, on right, after spinalization.

before spinalization, only less well synchronized, as shown by Figure 9. The greater spread of the spikes after spinalization agrees with the results of Ballif, Fulton and Liddell (1). Now, if one had been compelled to judge merely from the two monosynaptic curves alone, one would hardly have been able to forecast that the destructive effect of spinalization on the fringe would run parallel, with very little if any effect on the capacity of the centre to discharge.

Another way of demonstrating relative independence of fringe and active zone is to use ether in experiments of the type described. Thus in one case a heterosynaptic monosynaptic test volley of $295 \mu\text{V}$., which was facilitated during stretch to $1480 \mu\text{V}$., had been abolished by ether. Facilitation during stretch then gave a response of $90 \mu\text{V}$., meaning a reduction by ether in the ratio of about 16.5:1. The electromyograms did not appear to be correspondingly depressed, perhaps in the ratio of 5:1. The effect was reversible.

DISCUSSION

General comments. Referring to the schematic diagram of Figure 1, the experiments on spinalization and narcosis do not seem difficult to under-

stand. The motoneurons for a given stretch reflex are graded in potential excitability from highly active cells to fringe neurons at different levels of activity, the least excitable ones needing a great deal of external facilitation from a variety of polysynaptic sources (stretch receptors, other spinal and higher channels) to be able to respond positively to a "transmission test" such as the monosynaptic one used. A number of active neurons seem, however, to be activated so efficiently by stretch alone that they are relatively independent of whether the fringe is small or large, absent or present. Their facilitation up to discharge level takes place under practically all circumstances. Gauging excitability largely by measuring the number of fringe neurons does not therefore seem to be the right way of assessing the contribution of the active neurons to reflex activity as a whole.

Heterosynaptic testing may also run into difficulties when stretch at two states of initial tension are compared. An increase of tension often leads to greater reflex activity, as judged by electromyography and as is reasonable enough from what we know about muscle receptors (14, 20). This means facilitation. At the same time the fringe may shrink, signifying inhibition. We know that an increase of tension favors true autogenetic inhibition (7, 8, 9) which in several ways has been demonstrated to be of importance for the gastrocnemius system (2, 4, 7, 8, 9). In decerebrate animals this inhibition is nearly always concealed in stretch (contraction being a more potent stimulus for it) but it can be detected by its reciprocal effect on the knee flexors (4, 8). The discrepancy between the "discharge test" and the "transmission test" with change of muscle tension could be explained by the assumption that autogenetic inhibition removes a number of fringe neurons without succeeding in preventing the active neurons from displaying their full activity. We do not know why the fringe neurons are fringe neurons—whether because of paucity of excitatory end feet, because of excess of inhibitory innervation, or for some other reason—but we do know from direct measurements that they are more sensitive to inhibitory influences (9) than the active ones.

Another explanation would be to assume that in decerebrate animals heterosynaptic testing through one nerve can be influenced by reflex firing through the other. This amounts to stating that firing in certain ventral horn cells can depress the excitability not only in those cells that have fired but also in adjacent ones. Electrical interaction of this type has been demonstrated by Renshaw (24) with synchronized shocks. Eccles and his collaborators (2), using Dial animals and synchronized conditioning shocks, concluded that heterosynaptic testing differed from the homosynaptic method in not testing motoneuron depressions. Using stretch and both decerebrate and Dial animals, this point was taken up by one of us (C.J.) separately by the method of Hagbarth and Naess (10), according to which the reflex firing is stopped by inhibition from a preliminary shock to the antagonist deep peroneal nerve. Removal of firing released heterosynaptic facilitation. This depressor effect on adjacent neurons could, partly at least, explain why the heterosynaptic curve did not rise with the increased facilitation (ac-

accompanied by firing) after augmentation of muscle tension but recorded shrinkage of the fringe instead. The two explanations suggested, either of them by itself or both together, suffice to explain the discrepancies noted between heterosynaptic testing and electromyography.

Homosynaptic testing showed that secondary discharge periods in stretch generated less depression than the immediate firing. Later discharges would probably be given by the most active neurones alone. These are capable of fast recovery (9), differing in this respect from neurones at lower levels of excitability. The assumption that later discharge periods are predominantly run by active neurones is therefore a possible explanation of their less heavy depressions after firing. Secondary facilitations to stretch have also been noted by Magladery and his collaborators (22).

Methodological comments. Homosynaptic testing is complicated because of the combination of fringe testing with effects of depression (refractoriness and subnormality) in the motoneurones that have fired. The amount of firing must be considered. If negligible, there may be very little difference between homo- and heterosynaptic testing in stretch, as often seen with Dial cats (7). There is generally more firing in decerebrate cats. Eccles and his collaborators (2) with weak single conditioning shocks and Dial animals report motoneurone depressions also after reflexively subliminal stimuli in homosynaptic testing but do not find significant depression after heterosynaptic testing. As stated above, Job (13) has investigated heterosynaptic testing to stretch from this point of view and does find some depression also in heterosynaptic testing, even when visible firing is restricted to one gastrocnemius nerve, the other one being used for the test shock. Thus motoneurone depressions may be a complication also in heterosynaptic measurements of reflex excitability though less so than in homosynaptic ones. Homosynaptic testing is further complicated by peripheral or afferent refractoriness in the early phase of excitation by stretch or contraction. This leads to temporary diminution of the test shock. Depression on the afferent and efferent side of the arc is greater the greater the discharge and the more it is synchronized. This makes homosynaptic testing difficult to handle and often distorts the measurements unless the specific aim is to measure those depressions. The interesting work by Magladery and his collaborators on man (18, 19, 22), using monosynaptic testing with intrathecal leads for recording, is complicated by the homosynaptic method of measurement. The problem of finding representative test filaments is one more difficulty when homosynaptic testing is used the way it has been used above as well as in Magladery's work.

Heterosynaptic testing, being a method of sampling, is less dependent upon the choice of representative filaments. Far from being perfect, it is, nevertheless, often the ideal method for detecting a "submyographic" (or "subelectromyographic") change in the fringe beyond reach of the simple discharge tests. These, besides, are complicated by an unknown factor of small fibre reflexes (14, 15) and in many situations by antidromic effects as

well. The heterosynaptic test may, however, be a poor indicator when the fringe is small (spinalization, narcosis, possibly also pathological effects due to disease). It may also fail when, as occasionally happens, the monosynaptic control response is so large as to mobilize practically the whole fringe by itself. In the latter case the remedy is to reduce the strength of the test shock. The very large monosynaptic responses generally stand reduction to half maximum size without becoming irregular.

Most of the difficulties mentioned and exemplified disappear when the monosynaptic method is used with single ventral horn cells (9) but with this method the majority of problems require too much experimental work in order to provide enough information about the average behavior of the reflex center. It is a method for highly specific and circumscribed questions. For most purposes a combination of heterosynaptic testing with a discharge test (myography, electromyography) will be the best approach available today.

SUMMARY

The changes of reflex excitability have been measured in decerebrate cats during stretch by two methods: (i) monosynaptic testing in respectively homo- and heterosynaptic arrangement and (ii) electromyography. In order to be able to use the two methods in parallel, part of the ventral roots L7 or S1 have been severed and placed on the recording electrodes for the monosynaptic test while the intact portion of the roots was delivering the reflex impulses in response to stretch.

The aim of the work was to find out whether motoneurone excitability, as gauged by monosynaptic testing, corresponded to the actual excitability as measured by the amount of reflex discharge into the muscle.

The two methods of testing were found to be at variance in a number of instances described in the paper. Examples of such instances are: spinalization, stretch at different degrees of tension, ether narcosis. The discrepancy consisted in electromyographic recording, indicating very little changed or even increased reflex activity at a time when the monosynaptic test indicated diminished excitability of the motoneurons.

Homo- and heterosynaptic testing have been compared in order to elucidate the nature of this discrepancy. Various sources of error have been considered.

The basic explanation was found to be that a discharge test such as electromyography emphasizes the behavior of the active neurones whilst monosynaptic testing measures the size of the subliminal fringe which may be silent from the point of view of reflex activity.

The observations, apart from their methodological interest, are of importance for the definitions of reflex excitation and inhibition.

In homosynaptic testing it was noted that the reflex discharge in the beginning of stretch left a great deal more motoneurone depression than similar discharges later, during slowly developing stretch.

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