REFLEX SUMMATION IN THE IPSILATERAL SPINAL FLEXION REFLEX.

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SETSCHENOV 1868(21), Stirling 1874(29), James Ward(30) and Exner(11) were the first investigators of reflex activity to appreciate the importance of summation of repetitive stimuli. From a consideration of their results Goldscheider(16) regarded each neurone as presenting a definite threshold (the neurone threshold) over which the excitation produced by afferent impulses had to rise, *e.g.* by summation, before a discharge of the neurone was produced. The features of reflex summation were also well shown in the scratch reflex(22, 23). By this time division into the sub-groups of spatial and temporal summation had been well established; it was recognized that both forms depended on the central overlap of the effects of the excitatory stimuli, the locus of summation probably being the synapse. Lapicque(17) confirmed the central location of reflex summation, for he found it to be greatly affected by heating or cooling the spinal cord, while similar treatment of the afferent nerve gave negative results.

The essential basis of the division (18, 19) of reflexes into two classes—*d'emblée* and recruiting—depends on the extent to which the central effect of an exciting impulse is influenced by those which precede it. In a typical *d'emblée* reflex, the spinal flexion reflex, a succession of afferent impulses is unable to raise above threshold any more neurones than is a single impulse.

The duration of the excitatory process in those neurones excited below neurone threshold by a single impulse must be so short that it has disappeared before the next impulse arrives, else summation would be present, and a series of impulses would bring in additional motor units. In a recruiting reflex, the decerebrate crossed extensor reflex, on the other hand, a single stimulus is often ineffectual, and, with each repetition of the stimulus, more and more neurones reach the neurone threshold. The central excitatory process must be of such duration that

each successive impulse is able to add its excitatory effect to that remaining from the previous impulses until the neurone threshold is attained.

Here is a conception which implies that the duration of the central excitatory state varies greatly for different types of reflex. The purpose of the present work is to attempt to study by a more direct method the time relations of the central excitatory process following the arrival of a single volley of excitatory impulses at the neurone.

METHOD.

The animal (cats with the exception of two dogs) having been anæsthetized, any spinal cord operation necessary (division of dorsal roots or section of cord) was performed, immediately followed by decerebration by the trephine method. In some experiments the animal had been made spinal with aseptic precautions 4 to 6 days previously. Following decerebration, all the muscles except the one to be investigated were immobilized by appropriate nerve and tendon section, and the skin was denervated. The importance of as complete a denervation as possible has so impressed us that we have latterly considerably complicated our technique by extradural division of almost all dorsal roots belonging to the segments of isolated spinal cord whose reactions we were investigating with the exception of those in the afferent path of the reflex. Muscle immobilization by tendon resection is much less satisfactory than denervation, so, with all limb muscles except psoas, denervation has been performed. Skin has also presented problems, for the traditional operation does not denervate the skin in the gluteal region, which has been rendered insensitive in some recent experiments by section of the dorsal divisions of the lower lumbar spinal nerves. The aim of this extensive preparation was to free, as far as possible, the investigated reflex responses from all extraneous complicating stimuli.

The mirror myograph employed in our earlier experiments had a frequency of 660 D.V. per second, and, at the usual magnification of about 600, it gave an image movement of 5 mm. for 10 g. More recently we have used a myograph of similar sensitivity but with a frequency of 1300 D.V. per second. Such high sensitivity is necessitated by the weakness of the twitches which we have had to record. In later work electromyographic records with a Cambridge string galvanometer have been combined with the myographic: the bright myographic image registers photographically on the less bright background from the galvanometer optical system. All observations are measurements from photographic records taken by a falling-plate camera.

Care has been taken to control the temperature of the preparation, and all exposed tissues have been kept moist by warm Ringer.

Reflexes have usually been elicited by single break induction shocks applied to nerves kept under constant conditions by fluid electrodes (6) by which the nerve was stimulated as it lay in defibrinated blood taken from the animal itself. Single shocks at various time intervals were obtained by an electromagnetically released pendulum which was

reliable to $0{\cdot}1\sigma$ for intervals less than 16σ. A second excitatory stimulus has been used to sample the central condition at any particular interval after the first stimulus[1]. Under these conditions any difference in the response to the second stimulus depends on the central effects remaining from the first stimulus. To avoid complications produced by wave summation in the muscle (20, 15) by two stimuli following in quick succession, it was necessary to have the first stimulus at threshold intensity[2] (neurone threshold), and, for the purpose of further simplification, the second stimulus was also usually at threshold.

RESULTS.

The first experiments using complex nerves (superficial peroneal, anterior tibial, internal saphenous) as afferents had given such complicated results that it became necessary to choose our afferent nerves and our muscle so as to simplify the analysis as much as possible. All afferents from skin must necessarily be composed of fibres from such widely differing receptors as those for pain, pressure, touch, and temperature. It, therefore, seemed better to employ afferent nerves from muscles. When both stimuli are applied to the same afferent, it is impossible to rely on recovery from the relative refractory period following the first until 6σ has elapsed. The period from simultaneity to this interval was found to be of such interest and importance that it was essential for the second stimulus to be applied to a different afferent from the first. It is advantageous to choose closely allied afferents, as the amount of central overlap (occlusion) between them is greatest (5, 10). In the most instructive experiments we have used the two nerves to gastrocnemius (one to the medial head and the other to the lateral head and soleus) as afferents reflexly exciting tibialis anticus.

I. *Tibialis anticus.*

The method of experiment was to find the threshold for reflex excitation of tibialis anticus by a break-shock given by one pendulum key to one nerve to gastrocnemius (central end of cut nerve) and then by the other key for the other nerve. The two shocks, one to each, are then given at various intervals from simultaneity to one or the other leading

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[1] With the afferent nerves used the peripheral paths have been closely similar, *e.g.* two gastrocnemius nerves, dorsal digital nerves, or the two branches of peroneal used as pairs, so that the interval between the stimuli can be taken as equal to the interval between the arrival of the afferent volleys in the reflex centre.

[2] We have often used a strength of stimulus just above threshold, so that the smallest observable reflex response (1 to 2 g.) was obtained.

by such an interval that the preceding stimulus ceases to have any influence on that following. It is found that these two non-effective stimuli when combined in certain time sequences produce a reflex contraction of the muscle. Great care has been taken to exclude the following possible sources of this enhancement of the effect of one stimulus by the other.

(1) Physical effect of one electrical current on the other. The two secondary coils are placed about three metres apart at right angles to each other. The wiring of the primary and secondary circuits has been as straight as possible, and all wires are run as widely separated single core conductors. The effectiveness of these precautions has been shown by simultaneous breaking of both primary circuits with one secondary short-circuited, having exactly the same stimulating power as the shock from the unshort-circuited secondary alone.

(2) Spread of stimulus from one electrode to the other, or from either or both electrodes to the motor nerve, or to other afferents. The best safeguard against this danger was its ease of detection. It was shown[1] that the duration of effect of one break induction shock on motor nerve fibres was not longer than 0.5σ when the conditions of circuit, key, and coil were almost identical with those used in these experiments, so that the influence of the spread of one stimulus on the effectiveness of another could only last for this period. It has been very rare for the simultaneous stimulation of both afferents to differ in reflex effect by more than a slight amount from stimulation with either leading by 1σ, at which interval spread of stimulus could not be a complicating factor.

(3) A summational effect in the muscle itself whereby two or more stimuli in rapid succession give a larger effect than the sum of each individually (wave summation). Although apparently causing no reflex effect either stimulus alone may be reflexly exciting a few motor units whose twitch contraction is not registered by the myograph because (a) the inactive muscular mass exerts a damping effect, (b) the contracting muscle fibres are not initially taut owing to insufficient initial tension or to inequality of the tension distribution, (c) the frictional resistance of the myograph cannot be overcome by the very small torsional force. Effect (b) can be excluded because it has been found that further increase of the initial tension used (about 50 gr.) did not cause a subliminal stimulus to become liminal. The effects (a) and (c) are difficult to gauge, but, as electrical records show absence of action-

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[1] The secondary circuit was broken by one pendulum key at various intervals after the breaking of the primary circuit by the other pendulum key.

currents when the myogram shows absence of contraction, it seems that the interference is not great. The weak contractions undoubtedly suffer more than the strong, and hence the degrees of facilitation which we have shown are somewhat augmented. Moreover, the reflex facilitation curves have never resembled "wave summation" curves, so it seems certain that the curves we have obtained, while modified by the above factors, are in essentials independent of them.
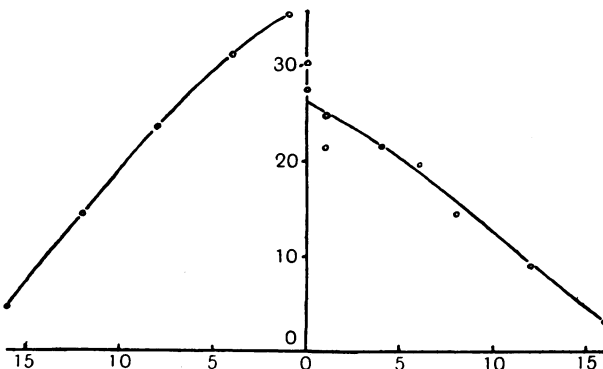

Fig. 1. Reflex responses of tibialis anticus to stimuli (alone just threshold) to med. gastroc. n. and lat. gastroc. n. at various intervals. Abscissæ = time in sigmata, ordinates = tension in g. To the right of zero is shown interval by which stimulus to lat. gastroc. n. is leading—to the left by which med. gastroc. n. is leading. (The response of the preparation altered somewhat between the observations on these two sides.) Each point plotted shows the tension developed at the indicated interval between the stimuli.

There remains the possibility of the facilitation of the central effect of one stimulus by that of the other. In Fig. 1 each point represents the tension developed by reflex contraction of tibialis anticus[1] in response to a just threshold stimulus of one nerve to gastrocnemius separated by the indicated interval from a just threshold stimulus to the other nerve to gastrocnemius (for convenience henceforth called med. gastroc. and lat. gastroc. nerves). It will be noticed that in this and other figures some of the points lie away from the curves which we have attempted to draw[2]. The degree of variability has been such that the

[1] The approximate proportion of the motor units of tibialis anticus brought into activity in any of the reflex twitches can be calculated on the assumption that the maximum motor twitch is about 400–500 g. for the type of animal used.

[2] Great care has been exercised, by random selection of intervals, to avoid any gradual change in the preparation affecting the shape of the curve. Usually at least one repetition of each observation has been made later in the series. All the observations of a consecutive series have been plotted in the curves shown.

actual shape of the smoothed curves can have little significance. We can only rely on such features as the position of optima and the degree of facilitation. The presence of "angles" in records from which the measurements have been made shows the influence of friction in the myograph bearing and warn against a too precise interpretation of the curves. Although the electrical responses of the muscle indicate that the reflex discharge is a single volley, a direct proportionality between tension development and excited motor units is an unjustifiable assumption. However, greater tension development will always indicate the excitation of more motor units. Hence, Fig. 1 will show that, when afferent impulses in med. gastroc. n. arrive practically simultaneously with those in lat. gastroc. n., more anterior horn cells belonging to tibialis anticus are excited supraliminally than at any other interval with these same strengths of stimulation.

In the further consideration of ipsilateral flexion reflexes it will be assumed that there is direct transmission from the afferent entering the dorsal root to the anterior horn cell with the intervention of only one synapse. This view is supported by the very short latency of these reflexes(13) and also by the transmission of high rates of rhythm from afferent to efferent(2, 4).

It is evident from Fig. 1 that the first stimulus though unable to excite any anterior horn cell sufficiently to cause it to discharge an impulse down its axis cylinder, nevertheless produces somewhere in the central path a state of raised excitability, for the second stimulus, which alone was able to excite no anterior horn cells, is now able to cause discharge from some when applied within a certain time interval from the first. One can think of the second stimulus as sampling the central condition remaining at various times after the first stimulus. As the stimuli are applied to different afferents which separately converge on the anterior horn cells, one would expect that, with simultaneous stimuli, there would be more central facilitation, for the central process being capable of summation cannot have a refractory period. Even if the central excitatory process took some time to develop, one would still anticipate that simultaneous arrival of impulses on the anterior horn cell would have an optimal effect, for the maximum central excitatory condition of each would be reached at the same time. But it is by no means usual to obtain such a simple facilitation curve as Fig. 1, curves such as Fig. 2 being more common. Here it will be noticed that there is a distinct optimum facilitation when the stimulus to med. gastroc. n. precedes that to lat. gastroc. n. by 12σ. When the stimuli are

applied in the reverse order, there is no sign of such an optimum. The complexity of the results is best indicated by a brief summary of the more successful experiments.

Exp. 21. xii. 28. Marked optimum with stimulus to med. gastroc. n. leading by 12σ (both stimuli threshold). When stimulus to med. gastroc. n. weakened and stimulus to lat. gastroc. n. increased to above threshold this optimum changed from 12σ interval to 6σ interval, though there was no marked falling away in response until the interval was greater than 12σ. No optimum was observed with stimulus to lat. gastroc. n. leading.
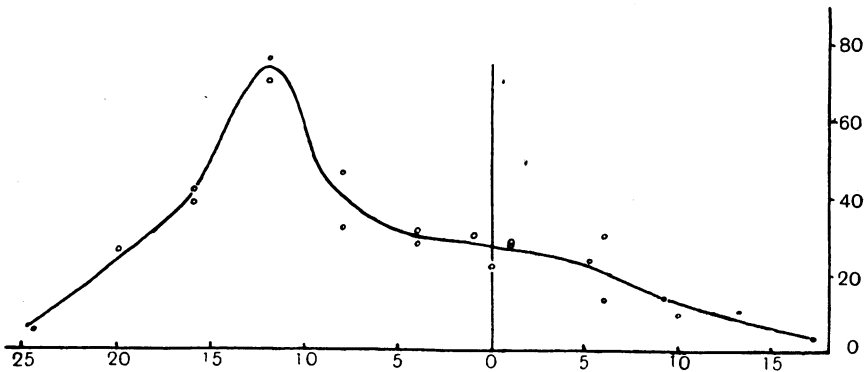
Fig. 2. As in Fig. 1 in a different preparation.

Exp. 7. i. 29. A well marked optimum with stimulus to lat. gastroc. n. leading by 12 to 14σ with a slight doubtful optimum at simultaneity.

Exp. 8. i. 29. At first there was an optimum with simultaneous stimuli. It soon changed and a well marked optimum with stimulus to lat. gastroc. n. leading by 13 to 14σ appeared (Fig. 3). Later the optimum at simultaneity returned and no trace of the optimum at 13 to 14σ interval remained.

Exp. 10. i. 29. A well marked optimum with simultaneous stimuli with no signs of optima at any other interval (Fig. 1).

Exp. 11. i. 29. This was the most instructive experiment and will be dealt with in more detail. Fig. 2 illustrates the curve obtained with both stimuli at threshold. All possible alterations in the strength of the stimuli failed to reveal an optimum with stimulus to lat. gastroc. n. leading, but an optimum at simultaneity was well marked under some conditions (Fig. 6).

Exp. 21. v. 19. Optimum at simultaneity.

Exp. 4. vi. 29. Three optima present: med. gastroc. n. stimulus leading by 12σ, simultaneity, and lat. gastroc. n. stimulus leading by 11σ.

To sum up: In three experiments an optimum occurred when stimulus to med. gastroc. n. was leading by 12σ (changed to 6σ in 1st exp.), in three others when stimulus to lat. gastroc. n. was leading by 11–14σ, and in six at simultaneity (one not well marked).

These results indicate that the central arrival of a volley of nerve

impulses in either the lat. gastroc. or med. gastroc. afferents can produce,
in the anterior horn cells of tibialis anticus, two excitatory conditions
with distinct time relations, one reaching a maximum almost im-
mediately and the other after about 12σ. This is made especially clear
in Exp. 8. i. 29, where one type of facilitation was entirely replaced by
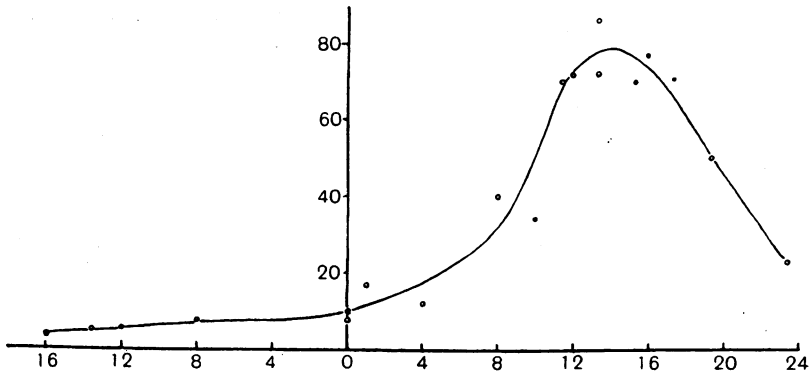the other and then later the reverse change took place. Fig. 3 shows the

Fig. 3. As in Fig. 1 in another preparation.

definite optimum existing at 14σ, of which no trace could be found 2 hours
before or 2 hours after, it being replaced by the optimum at simultaneity.
Unfortunately the preparation was not under investigation during the
transition period, but it seems likely that it was due to slight changes
in the relative excitability of the nerve fibres causing an alteration in
the nerve fibres stimulated.

     After Fig. 2 (in Exp. 11. i. 29) had been obtained both stimuli were
applied to the med. gastroc. n. Although the relative refractory period
would interfere with the stimuli less than 6σ apart, still the optimum at
12σ should remain; but the curve shown in Fig. 4 was unexpectedly
found. A return to the original observation showed that the type of
curve with an optimum at 12σ was still being given. Thus different
sampling afferents give evidence of different excitation after-effects
following the first stimulus.

     As each anterior horn cell will not be played upon in the same way
or to the same extent by each afferent, and, doubtless, some anterior
horn cells will only be played on by one afferent, this condition would
be expected to some extent. But no such wide divergence as is here
represented can be completely explained by such a consideration. In
Fig. 4 the second stimulus is of equal intensity to the first, so that all

the anterior horn cells stimulated by the first will also be stimulated by the second. How is it, then, that no evidence is obtained of those anterior horn cells which sampling by lat. gastroc. n. shows to be most excitable 12σ after the stimulus to med. gastroc. n.? Fig. 5[1] will make the argument clearer. The area enclosed by the outer circle represents all the
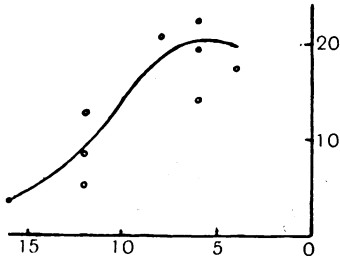

Fig. 4.   Fig. 5.

Fig. 4. As in left-hand side of Fig. 2 except that both stimuli were applied to med. gastroc. n. Registered immediately after Fig. 2.
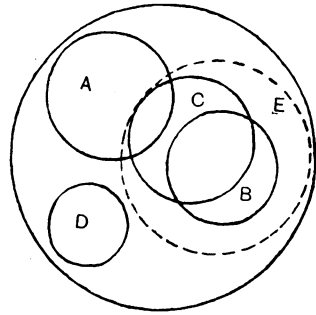
Fig. 5. Diagram, explanation in text.

anterior horn cells of tibialis anticus and a small area A corresponds to those neurones on which the subliminal central excitatory effect of threshold stimulus to med. gastroc. n. is exerted. Area B represents the neurones on which a delayed effect is exerted by the same stimulus. This delayed effect reaches its maximum 12σ after the arrival of the stimulus. It must be understood that this is purely diagrammatic, and it is very unlikely that any strict topographical localization exists in the spinal cord. Areas A and B probably do not overlap, for, when the effect of a stimulus to med. gastroc. n. is sampled by a similar stimulus, there is no indication of an optimum at 12σ interval[2] (Fig. 4). In the same diagram area C could represent those neurones subliminally excited by the stimulus to lat. gastroc. n. There will be two distinct time processes involved. (*a*) That having an optimum at simultaneity and steadily diminishing as the interval is increased (overlap of C with A). (*b*) That having an optimum at 12σ (overlap of C with B).

[1] Areal representation conveniently depicts by overlap units common to two afferents, as evidenced by the occurrence in them of summation.

[2] The non-existence of the optimum at 12σ interval is not a certain proof of the absence of overlap of areas A and B. Complications are introduced if the delayed excitation is a rebound following the initial inhibition (see pp. 10, 14), for then the tendency to rebound in area B following the first stimulus would possibly be prevented by the initial inhibition of the second.

Though the curve of Fig. 2 does not seem to be composed of two distinct curves, several other curves obtained under similar conditions in that experiment showed a decided minimum at 4 to 8σ clearly separating two optima, *e.g.* Fig. 6, though there the conditions are not so constant.
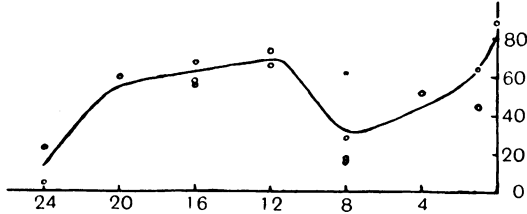

Fig. 6. Taken on same preparation as Fig. 2, but earlier in the experiment.

When the sequence of stimuli is reversed, as on the right-hand side of Fig. 2, we see that the reflex response steadily diminishes from simultaneity till it becomes almost negligible at an 18σ interval. Its simple form can easily be explained by the overlap of C and A already postulated to explain facilitation at intervals close to simultaneity. The delayed effect of any area D produced by stimulus to lat. gastroc. n. obviously does not overlap with the excitatory effect of med. gastroc. n. (area A).

When the central excitatory condition following the threshold stimulus to lat. gastroc. n. was sampled by a second similar stimulus, a curve of the type of Fig. 4 was obtained with an optimum at 6σ, values at intervals less than this probably being diminished by the influence of the relative refractory period of the afferent nerve. As no facilitation in the region of 12σ was obtained, it seems that the delayed effect of lat. gastroc. n. (if any) does not overlap with the excitatory, *i.e.* area D with area C. Such a condition would not be improbable, for an unphysiological act, such as electrical stimulation of an afferent nerve, is quite likely to excite afferent nerve fibres having different effects on the same anterior horn cell.

Denny-Brown and Liddell[8] found that the ipsilateral extension reflex in the fore-limb (supraspinatus) possessed a long latency—60σ; evidence showed that the delayed central excitation was really a rebound following a preliminary inhibition. To test whether a similar explanation would apply in our case, we intensified the sampling stimulus to lat. gastroc. n. so that it alone produced a moderate response. If inhibition were present one would expect that, when the med. gastroc. n. stimulation just preceded lat. gastroc. n., the reflex response would

be less than that to lat. gastroc. n. alone (Fig. 8). Such was not the case nor was there any sign of an optimum at 12σ interval. This is probably due to lat. gastroc. n. exciting above threshold all those neurones of area *B* (as shown by dotted circle *E*), so that the facilitation produced by their delayed excitation was now occluded. (With intermediate strengths of stimuli the optimum at 12σ emerges from the background excitation.) The presence of an inhibitory effect following immediately

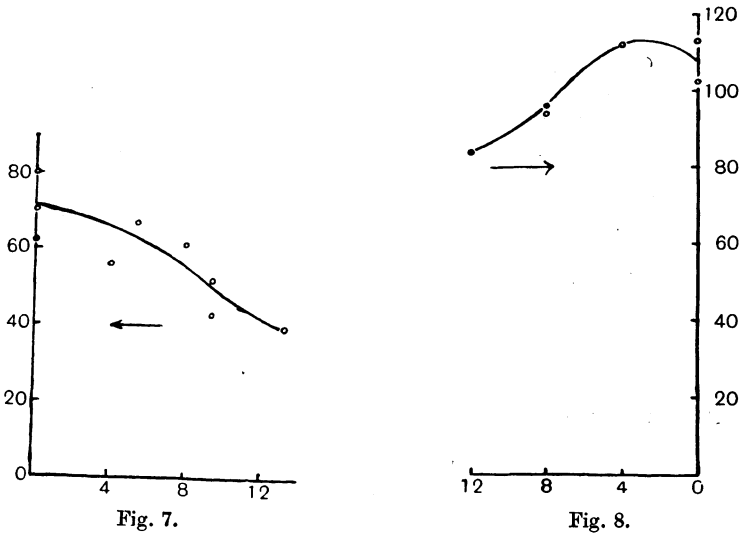
Fig. 7.   Fig. 8.

Fig. 7. As in right-hand side of Fig. 2 except that stimulus to med. gastroc. n. was now increased so that it produced a reflex twitch of 40 g., marked by arrow.

Fig. 8. As in left-hand side of Fig. 2 except that stimulus to lat. gastroc. n. was now increased so that alone it evoked a reflex twitch of 80 g., shown by arrow.

on the central arrival of the afferent volley from med. gastroc. n. and later rebounding as the delayed excitation, was not disproved by this negative evidence, for it was quite possible that the increase of stimulus to lat. gastroc. n. was able to produce a central excitation sufficiently strong to completely overcome any such inhibition. The existence of facilitation from simultaneity to about 12σ is evidence that the above threshold neurones for lat. gastroc. n. do not extend to the whole of area *A*, there being still an overlap of subliminal excitation corresponding to the original overlap of *C* and *A*.

The simple type of curve shown on the right side of Fig. 2 still persisted when the sampling stimulus to med. gastroc. n. was strengthened

(Fig. 7), showing that increase of area A still failed to overlap the hypothetical area D. That such an area can exist is shown by the results of Exps. 7. i. 29 and 8. i. 29, where optima with the stimulus to lat. gastroc. n. leading by 12 to 14σ are present (Fig. 3).

Evidence of the existence of rebound in tibialis anticus centre following stimulation of gastrocnemius afferents has been found in the only experiment (21. xii. 28) where the preparation was examined in the decerebrate condition before being made spinal. Even quite strong stimulation of med. gastroc. n. or lat. gastroc. n. with single shocks produced no reflex response in tibialis anticus, but, with tetanic stimulation (40 per sec.), it was found that rebound followed quite weak stimuli which during their application had produced no reflex response. The rebound was equally well marked with either nerve, though, in the spinal animal, an optimum at 12σ was only obtained when the stimulus to med. gastroc. n. was leading. In this case it seems clear that either afferent is capable of exerting an inhibitory effect on tibialis anticus even when stimulated quite weakly, for rebound is recognized as a sign of preceding inhibition. All trace of this rebound disappeared immediately after section of the spinal cord, and weak stimuli now elicited strong reflexes.

Analysis of reflex influence of gastrocnemius on tibialis anticus.

Denny-Brown[7] has found that taps to the gastrocnemius-soleus tendon sometimes produced twitches in tibialis anticus with a latency of just over 20σ. He suggested that this might possibly be the reciprocal accompaniment of the silent period in the extensor muscle. We have confirmed these observations in the de-afferented spinal tibialis anticus and have found that the latent period has been remarkably constant, 19 to 21σ in the cat and 24 to 26σ in the dog (medium size).

In all preparations we have observed that the tibialis anticus twitch has been more closely related to the strength of the tap than to the size of the gastrocnemius-soleus jerk. A typical delayed twitch in tibialis anticus has even been found where there was no gastrocnemius-soleus response following the tap. After completely cutting all the motor fibres to gastrocnemius and soleus (by severing the appropriate anterior roots, the dorsal roots remaining intact), it has been found that tapping the gastrocnemius tendon still evokes a twitch in tibialis anticus. It therefore seems certain that part, at least, of the tibialis anticus twitch must be a direct reflex response to the tension rise following the tap to gastrocnemius tendon.

If excitation of the muscle-spindles of gastrocnemius-soleus were

responsible for the tibialis anticus twitch, then stimulation of the anterior roots of the spinal nerves supplying gastrocnemius-soleus should also produce reflex twitches in tibialis anticus. Moreover, the latency of the response should be less than the twitches following taps to gastrocnemius tendon as the path is now shorter (Fig. 9). Thus from A (tendon-
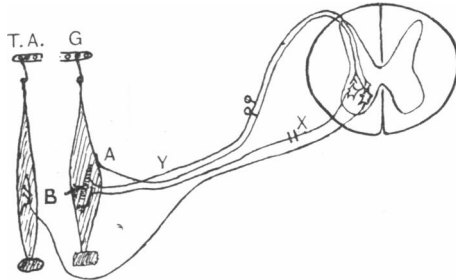

Fig. 9. Diagram of reflex paths connecting gastrocnemius (G)
to tibialis anticus ($T.A.$). See text.

organ) to gastrocnemius anterior horn cell, to B (muscle-spindle) back to tibialis anticus anterior horn cell and then out to tibialis anticus would be the path following a tap to gastrocnemius tendon, while, when the motor fibres of gastrocnemius-soleus muscle were stimulated at X, the path would be directly from X to B and then as before. The 8th post-thoracic anterior root usually contains no motor fibres for tibialis anticus, and, as it supplies at least 30 p.c. of those to gastrocnemius-soleus, it is the root we have chosen for stimulation. In two preparations a direct motor response in tibialis anticus (as shown by a latency of 4 to 6σ in the electrical and mechanical effects) spoilt the experiment. In four other experiments motor twitches in gastrocnemius-soleus were un-accompanied by any contraction in tibialis anticus, though less powerful contractions of gastrocnemius-soleus in response to tendon taps were regularly associated with twitches in tibialis anticus. This result is difficult to reconcile with the view that muscle-spindle excitation is responsible for the tibialis anticus twitch.

In only one experiment was there a twitch in tibialis anticus asso-ciated with the gastrocnemius-soleus contraction following 8th anterior root stimulation (only gastrocnemius-soleus contracted as the motor nerves of all other muscles supplied by 8th anterior root were cut). Plate-fig. 1 shows the long latency (greater than 40σ) and repetitive nature of the tibialis anticus response. In this preparation we have two reflexes produced in tibialis anticus from gastrocnemius.

(1) A tap to gastrocnemius tendon evokes a twitch in tibialis anticus with a latent period of 19–20σ.

(2) Following a twitch in gastrocnemius-soleus there is a repetitive response in tibialis anticus with a latent period of just over 40σ.

As we have already seen that the tap to gastrocnemius tendon can reflexly excite tibialis anticus, it is reasonable to suggest that the tension produced by the twitch reflexly excites tibialis anticus in the second case. In the former the afferent nerves from the tension receptors would be stimulated within a fraction of a sigma of the onset of the tap, while in the latter the extra delay of 20 or more sigmata would be due to the time elapsing during the passage of the nervous impulse from the anterior root to gastrocnemius-soleus and the subsequent development of active tension to an intensity sufficient to excite the appropriate tension receptors. In most experiments the active rise of tension is not sufficient to evoke any tibialis anticus reflex response, for it is much more gradual in onset than the passive tension produced by the tap. The comparatively long-continued rise of active tension in the motor twitch would explain the repetitive nature of the reflex response under these conditions.

It was surprising to find that, when no resistance was offered to the contractions of gastrocnemius-soleus, there was still a reflex in tibialis anticus which was, however, much diminished (4 a). It seems to show that tension receptors are stimulated by a muscular twitch even when there is no external tension development.

The latent period of the tendon jerk in gastrocnemius averages about 10σ, and of this interval about 8σ can be accounted for in the peripheral path. For the tibialis anticus reflex the afferent path is the same as for the gastrocnemius jerk, and the efferent path is not greatly different. Why, then, is there a latency of 10σ longer, leaving a central time of 12σ to be accounted for? It is here that one calls to mind the frequency of an optimal facilitation existing at an interval of 12σ in the facilitating effect of one gastrocnemius afferent on the other. At this interval of 12σ after the arrival of the afferent volley, the central excitatory state is at its maximum, and consequently the discharge down the axis cylinder is most likely to occur then. The presumption is strong that the tension afferents of gastrocnemius-soleus are responsible for the optimal facilitation at 12σ.

What is the reason for this long delay? In the ipsilateral extension reflex it has been shown (8) that the long latency is due to the twitch really being a rebound following an inhibition; it is possible that the same explanation also applies to this case.
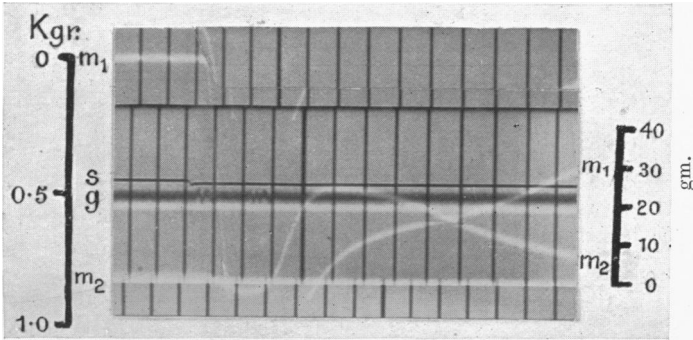
Plate-fig. 1. Reflex contraction of tibialis anticus in response to the muscular contraction of gastrocnemius-soleus evoked by stimulation of 8th post-thoracic anterior root. m_1 =myogram of gastrocnemius-soleus [pulling downwards (off the field at bottom of figure)—tension scale to left]; m_2 =myogram of tibialis anticus (pulling upwards—tension scale to right). The slight early fall in base line is due to give of fixation of limb caused by the strong gastrocnemius-soleus twitch. s =signal showing time of break-shock to 8th anterior root. g =string-galvanometer record—leads in tibialis anticus. The early action-current is due to spread of the strong action-current from the motor twitch in gastrocnemius-soleus. The delayed action-current shows the response of tibialis anticus with a latent period of about 40σ. Time between vertical lines $=20\sigma$.
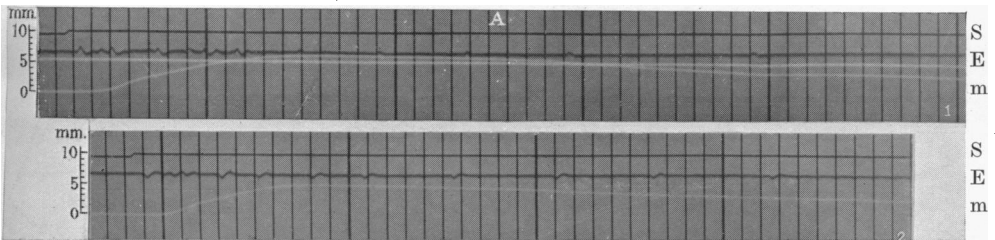

Plate-fig. 2. A record of response of tibialis anticus (de-afferented and with motor roots largely cut down) to a single stimulus to the ipsilateral sciatic nerve as shown by signal S. m shows myograph and E electrical record. From a chronic (8 months) spinal dog.

The development of central excitatory state in the anterior horn cells of tibialis anticus following a twitch in the lateral head of gastrocnemius and soleus has been investigated by sampling with a just liminal stimulus applied to the central end of the cut med. gastroc. n., *i.e.* by a technique similar to that used in investigating the central excitatory state following a nerve stimulus. Fig. 10 shows that there
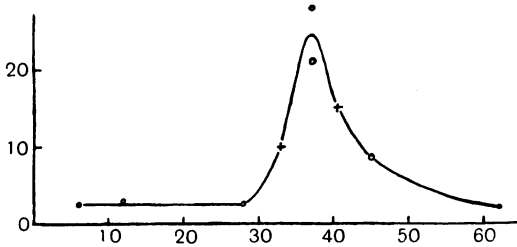

Fig. 10. As in previous graphs except that interval is now between first stimulus which is applied to the 8th anterior root, and the second stimulus which is applied to central end of cut med. gastroc. n. The tensions indicated for the two points marked by crosses are only approximate as they are not measurements of photographic records, but only values obtained by inspection.

was no sign of facilitation until the interval was greater than 28σ. The optimal facilitation occurred at 37σ interval; the effect then declined, and was over by 60σ. If this optimum at 37σ corresponds to the optimum at 12σ interval when one stimulus is applied to one gastroc. nerve and one to the other, there is an interval of 25σ between the stimulus at X (Fig. 9) and the arrival of the ensuing afferent nerve impulse at a point Y corresponding to the point where the stimulus is applied to the other gastrocnemius afferent. As the total latency of the tibialis anticus contraction was between 40 and 46σ, there is still an interval of about 18σ to be accounted for. This would correspond with a latency of 19 to 20σ in the tibialis anticus response to a tap to gastrocnemius tendon, and so support the view of the identity of the two reflexes. Fig. 10 bears a close resemblance to the delayed optimum facilitation curves of Figs. 2 and 3.

We have not succeeded in identifying the type of afferent fibre from gastrocnemius which is responsible for the immediate increase in central excitatory state, *e.g.* Fig. 1. It is not likely to be the muscle-spindle afferent, for the excitation of muscle-spindles from the anterior root does not seem able to produce reflexly any tibialis anticus contraction.

The time relations of the facilitation process distinguish between two types of central excitatory state.

(a) *The "direct" central excitatory state.* The excitatory effect on the individual anterior horn cells of tibialis anticus produced by a just threshold stimulus applied to one of the gastrocnemius nerves, *e.g.* area *A* (Fig. 5), will show all degrees of gradation from the smallest quantum of excitation to a condition of excitation just short of that where the cell discharges an impulse down its axis cylinder (neurone threshold). The intensity of the excitatory process in any neurone is certainly dependent on the number of excitatory impulses it receives, but it is not known whether a direct proportionality exists, for it is possible that the excitatory effect from some endings on the surface of the neurone is greater than that from others (*e.g.* (25), p. 524). In the response to a single stimulus these impulses will arrive practically simultaneously—a slight spread will be occasioned by differences in the path, and also in the speed of propagation, but it does not seem likely that delay paths can be of much significance in a cord sectioned in the upper lumbar region. The method of sampling used here necessarily only gives evidence of the existence of this subliminal excitatory state when the additional excitation of the sampling stimulus raises the excitatory level above threshold. Since it is found that, when both stimuli are applied together (and therefore reach the neurones in question practically simultaneously, for the central and peripheral paths are almost identical), the above-threshold level is attained in the most neurones, and the greater the interval between the stimuli, the fewer the anterior horn cells discharging, it must be concluded that the excitatory level produced by the first stimulus reaches its maximum with great rapidity (also shown by the brevity of the reduced reflex time of the flexion reflex) and then gradually declines. The lessened degree of facilitation at increasing intervals merely indicates that fewer neurones can now be raised above threshold by the second stimulus, and hence shows that, in the individual neurones, the excitatory state following the first stimulus is decreasing. The facilitation curves which we have obtained are only indirect statistical indicators of changes in the central excitatory state in the individual neurone. Though Fig. 1 shows practically no facilitation at 16σ, it does not indicate that the excitatory state produced by the first stimulus has then completely disappeared, for in those neurones where it still persists the sampling excitation may not be of sufficient intensity to enable the summated effect to reach threshold. It seems very probable that the central excitatory state persists longest in those neurones where it is initially most intense. A duration of 8 to 10σ usually obtains a few hours after spinal transection. This often increases to 20 or more sigmata

in the course of 24 hours. The lengthening with the longer period of recovery is probably a manifestation of the passing off of spinal shock. A duration of 20σ seems somewhat surprising for a subliminal excitation in a spinal flexor reflex, and doubtless with stronger excitation the duration is much longer, thus giving the explanation of the after-discharge following a single stimulus(24) and of the secondary waves in a tetanic response(1, 4).

Plate-fig. 2 is an extreme example of the long continued repetitive response in an ipsilateral flexor reflex. The spinal cord was transected 8 months previously and immediately before the experiment the muscle was completely de-afferented and most of its motor fibres were cut by almost complete division of the anterior roots supplying it. At first there are indications of action-currents in more than one motor unit, but soon one type of action-current alone remains, the intervals between successive firings increasing until an abrupt stoppage takes place. The view that one unit was responsible for these action-currents was strengthened by finding that alterations in the positions of the leads changed their shape without altering their identity in any particular record.

(b) *The delayed central excitatory state.* Usually its rise and decline are fairly abrupt. Though remarkably constant in its optimum time, it often shows a rather large degree of irregularity in tension development, *i.e.* in the number of discharging neurones. No differences other than degree of tension development can be seen between the myographic curves obtained at simultaneity of both stimuli and those with the optimum interval of 12σ. The delayed curve uncomplicated by the excitatory curve is shown in Fig. 10 where 25σ is equivalent to zero time (*v.s.* p. 15). It will be seen that, for at least 3σ later, there is no increase in the central excitatory state. This shows that, here, the initial central effect of the afferent impulses is not excitation and suggests that the delayed excitatory state may be a rebound following a short preliminary inhibition, though such an inhibition could not be demonstrated directly (*v.s.* pp. 10, 11). A rebound in 12σ is admittedly earlier than any yet described, but one must bear in mind that it is in a flexor muscle while other rebounds of this type have been in extensors.

II. *Semitendinosus.*

Various pairs of nerves have been used as afferents for reflexly exciting semitendinosus. As before, threshold stimuli were usually employed.

Spinal semitendinosus. (a) Superficial peroneal and anterior tibial nerves when used as afferents gave reliable results on three occasions.

Exp. 22. i. 29. There was a definite optimum when the stimulus to anterior tibial nerve preceded that to superficial peroneal nerve by 4σ (Fig. 11). The dip towards simultaneity
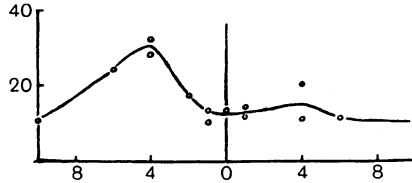

Fig. 11. Reflex responses of spinal semitendinosus to stimuli (just threshold) to anterior tibial and superficial peroneal nerves. Abscissæ show stimulus interval in sigmata. To the left of zero anterior tibial is leading, to the right superficial peroneal.

is curious, and indicates that, when the stimuli arrive at the anterior horn cell together, they have less effect than when separated by a small interval. When the stimuli were employed in reverse time relationship, there was one doubtful value giving a slight rise at 4σ, but it was not confirmed by repetition. When the stimuli to either or both nerves were increased, with anterior tibial leading there was still the same optimal interval of 4σ.

Exp. 17. xii. 28. In this experiment, 1 to 2 hours after cutting the spinal cord, there was a definite optimum with stimulus to anterior tibial nerve leading by 2 to 3σ. With simultaneous stimuli the degree of facilitation was quite small.

Exp. 13. iii. 29. Spinal dog, cord cut 6 days previously. The optimum occurs with stimulus to anterior tibial nerve leading by 2σ (Fig. 12). It agrees well with the previous
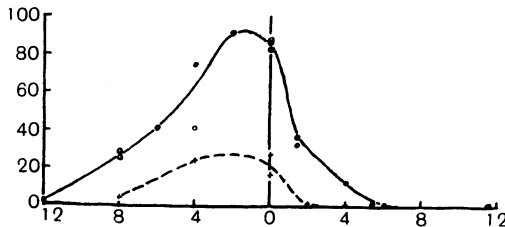

Fig. 12. As in Fig. 11, but in a chronic spinal dog (cord cut 11 days previously). To the right of zero superficial peroneal is leading, to the left anterior tibial. The dotted record and the crosses show the curve when the stimulus strength was weakened.

experiment in the short duration of facilitation existing when the stimulus to superficial peroneal nerve was leading. This curve was essentially unaltered by weakening both the stimuli. A definite second optimum was later found with anterior tibial stimulus leading by 16 to 20σ separated from the original optimum by a minimum of 14σ.

There is general agreement in there being a much greater and more prolonged facilitation when the stimulus to anterior tibial nerve precedes that to superficial peroneal, and this peculiarity is independent of the strengths of stimuli employed. The significance of this variation is

unknown, but it shows definitely that the afferents employed have complex central effects. These are to be expected from afferents having nerve fibres from both muscle and skin. The delayed rise in the last experiment again suggests rebound.

(*b*) In the hope of simplifying the complex conditions of the experiment, it was decided to try the effect of two pure skin nerves on each other. After dissecting up and cutting short the muscular branch of superficial peroneal, the remaining pure skin afferent nerve was split. It was easy to do this in all but one exceptional case, for, on incising the sheath, the four dorsal digital nerves were found lying discrete each from the others. Usually we separated the lateral two from the medial two.

Exp. 5. ii. 29. About 3 hours after section of the spinal cord there was a small degree of facilitation with simultaneous stimuli which diminished rapidly as the interval between the stimuli was increased. This is a type of early shock curve which we have found with many different afferents and with both semitendinosus and tibialis anticus as test muscles. Three hours later a totally different curve (Fig. 13) was obtained with similar strengths of
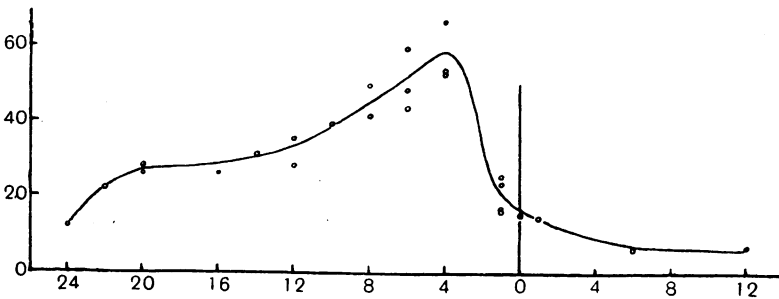

Fig. 13. Reflex responses of spinal semitendinosus to stimuli (just threshold) to lateral and medial divisions of superficial peroneal nerve, *i.e.* dorsal digital nerves. To the left of zero medial dorsal digital division is leading, to the right the lateral division.
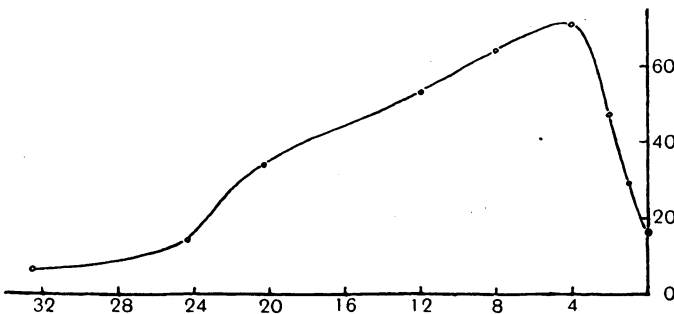

Fig. 14. As in Fig. 13, but stimulus to lateral dorsal digital increased so that just above threshold. Curve shows results with only medial dorsal digital division leading.

2—2

stimuli. The abrupt fall towards simultaneity from the optimum at 4σ is remarkable and resembles the curve when anterior tibial and superficial peroneal nerves were used as afferents. (Observations taken a little later confirmed the curve between 4σ and 1σ.) There is practically no facilitation when the stimulus to the lateral division leads by more
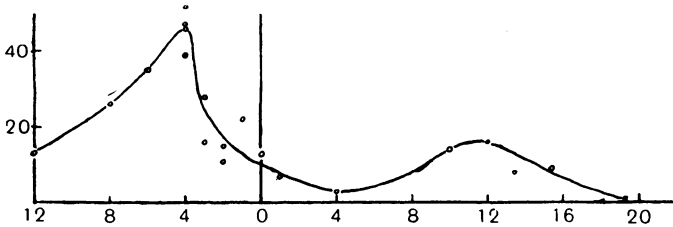

Fig. 15. As in Fig. 13, but stimulus to medial dorsal digital increased so that just above threshold, lateral dorsal digital stimulus being considerably below threshold. There is here an additional optimum when stimulus to lateral dorsal digital leads by about 12σ.

than 6σ. With the stimulus to the medial division leading there is considerable facilitation even at 20σ interval, beyond which an abrupt falling off occurs. Till the end of the experiment (3 hours) this very characteristic and grossly asymmetrical curve was found to remain unaltered in its essential features, when the strengths of stimuli to either afferent or both were increased or diminished (Figs. 14 and 15). Moreover the curves obtained
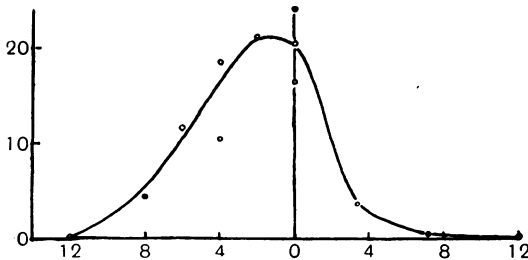

Fig. 16. As in Fig. 13, but in another preparation (about 2 hours after cutting of spinal cord). Just threshold stimuli.
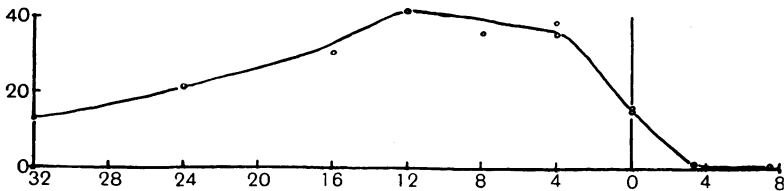

Fig. 17. Same experiment as Fig. 16 but about $2\frac{1}{2}$ hours later.

when both stimuli were applied to the same afferent gave evidence, that, if the influence of refractory period could be allowed for, there would be essential similarity between them and the curves obtained by sampling each by the other afferent. When the effect of the stimulus to the lateral division was sampled by a similar stimulus, there were practically no signs of facilitation at any interval.

Exp. 11. ii. 29. About 2 hours after spinal section there was an early shock curve (Fig. 16) similar to that in the previous experiment; 2 hours later a curve (Fig. 17) similar to
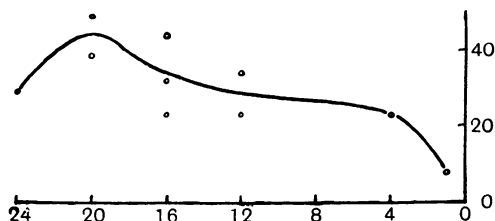

Fig. 18. About 1 hour later than Fig. 17. Only curve with medial
division leading shown.

Fig. 13 was obtained, but with further continuation of the experiment the optimum was found to extend further out until it was at 20σ (Fig. 18). There was still a considerable degree of facilitation at 4σ which dropped sharply to simultaneity.

Exp. 12. ii. 29. A well developed optimum was present when the stimulus to the lateral division preceded that to the medial division by 8σ. The identity of the nerve bundles split was, however, not quite certain owing to a twist in the nerve.

The sudden diminution in facilitation which is obtained so frequently when the interval is decreased from 4σ to 0 is puzzling. Is it possible that two stimuli arriving in quick succession have a greater exciting power than when they arrive simultaneously? The time interval seems too short to be explained as a rebound. Whatever the process is, it is depressed after spinal transection, for it usually does not appear till 5 or 6 hours have elapsed. The limit for the demonstration of facilitation is usually 20 to 30σ. As yet no analysis, such as that attempted for the experiments on tibialis anticus, is possible, but it seems likely that the early shock curve is the manifestation of the simplest type of response, and that more complex conditions arise as spinal shock disappears.

A series of other experiments on spinal semitendinosus served to show that facilitation could be obtained between such widely different afferents (*i.e.* muscle or skin segmentally widely apart) as nerve to vastus lateralis and superficial peroneal (with its muscular branch destroyed), or internal saphenous and superficial peroneal.

Decerebrate semitendinosus. It was on semitendinosus in the decerebrate animal that we first started our investigations on the time relations of the excitatory process. In our first experiments both stimuli were applied to the superficial peroneal nerve, and therefore suffer from the interference of relative refractory period at intervals less than 6σ. Both, however, showed curves with a definite optimum which in one case was

at 12σ interval and in the other from 13σ to 20σ according to the strength of the stimulus.

When superficial peroneal and anterior tibial nerves were used as afferents, complicated results were obtained, e.g., optimum intervals with either leading by 10σ to 14σ, and only once in the four experiments was there any indication of an optimum at simultaneity. In one experiment there were two optima with the stimulus to superficial peroneal leading, one at 2σ the other at 6σ to 10σ separated by a definite minimum at 4σ. The complexity of the central conditions is indicated by the compound nature of the time relations characterizing the central disturbance following a single afferent volley. One of the complicating factors is the inhibitory influence exerted on the flexors by the higher centres; this gradually increases after decerebration until often the flexion reflex is inelicitable. An immediate fall in reflex threshold follows abolition of this influence by section of the spinal cord (12, 20, 28). In the decerebrate animal the high threshold of the reflex response to a single stimulus, combined with a marked facilitation 10σ to 20σ after an ineffectual stimulus, can certainly be correlated with the recruiting nature of the reflex response of semitendinosus, for each preceding stimulus would facilitate the following until threshold was attained.

Besides causing an abrupt fall in threshold, spinal transection alters the form of the facilitation curve, but it is not certain how much this can be explained by the great difference in the strength of the stimuli used. In Exp. 4. xii. 28 a curve (Fig. 19) was obtained with a stimulus
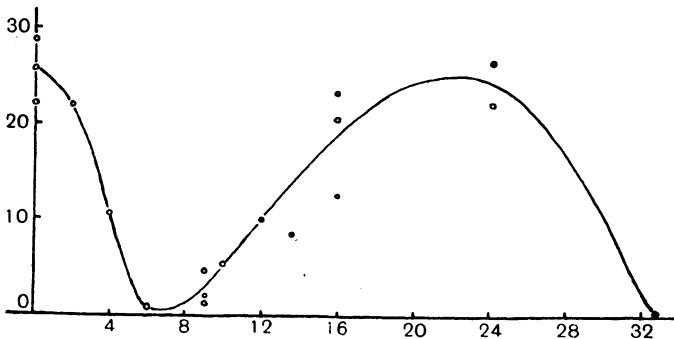

Fig. 19. Decerebrate semitendinosus responding to stimulus to superficial peroneal nerve followed by one to internal saphenous nerve. (Both stimuli below threshold.)

to superficial peroneal followed by one to internal saphenous (both stimuli at 12 cm. coil distance, either alone just threshold). When the

cord was transected, the threshold fell to 30 cm. coil distance for superficial peroneal nerve and to 26 cm. for ·internal saphenous. There was no sign of the previous optimum at 15σ to 25σ, there being only the typical early shock curve (Fig. 20). Previously to the cord section a
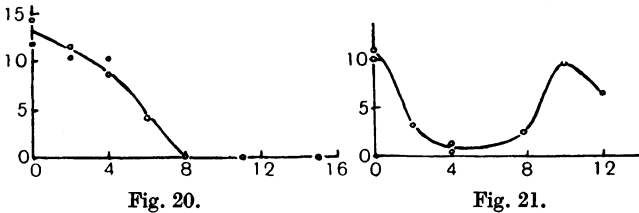

Fig. 20. Fig. 21.

Fig. 20. Same as Fig. 19, but spinal cord cut about ½ hour previously; stimuli just threshold, but much weaker than for Fig. 19.

Fig. 21. As in Fig. 20 but just before cord cut. The stimulus to superficial peroneal is the same strength as that used in Fig. 20.

curve had been obtained with the stimulus strength of superficial peroneal at 30 cm. coil distance (Fig. 21), and though then the second optimum was at 10σ, the shape of the curve was essentially similar to Fig. 19. Moreover, in the spinal condition, increase of the stimulus to internal saphenous nerve to a strength well above threshold (26 cm.) failed to show any sign of the second optimum. In this case it seems certain that spinal transection had removed the influence responsible for the second optimum.

The frequency of optima at intervals of about 12σ has been a feature with decerebrate semitendinosus, and raises the question of the essential similarity to the rebound phenomena in tibialis anticus. Unfortunately the mixed character of the afferents has rendered impossible any analysis of even the fragmentary character of that forthcoming in the case of tibialis anticus.

The following experiment was designed to distinguish between the threshold of the afferent nerve and the threshold of a reflex evoked by stimulation of it. Posterior tibial nerve was split for a considerable distance into two divisions M and L, the median and lateral plantar nerves; the calcanean branch was dissected up and cut short. It was possible to do this without injury as these components are in separate sheaths. Two electrodes A and B were now applied to the split nerve as shown in Fig. 22 and the reflex threshold (for ipsilateral spinal reflex in tibialis anticus) was determined for each, and was observed for some time until it reached a constant value, which was 60 cm. coil distance

for A and 33·9 cm. for B. Division L was now cut at X, care being taken
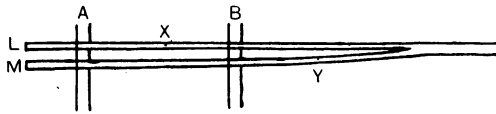not to disturb the nerve between either pair of electrodes. The threshold

Fig. 22. Diagram, explanation in text.

at A was now found to have risen to 58 cm. in the course of about
2 min. The excitation from the cut nerve was probably responsible for
this delay. One would infer from this increase of threshold that the
lowest threshold fibres were in the cut division L. The threshold of B
was found unaltered. Division M was then severed at Y with similar
precautions and the threshold at B was found to increase to 33·2 cm.,
again in the course of about 2 min. As before one would now infer that
the lowest threshold fibres were in division M. As it seems unlikely that
there is an alteration in the relative excitability of the fibres of L and
M divisions over so short a distance as AB, one must accept the
alternative that the thresholds measured were not afferent fibre
thresholds but neurone thresholds. The lowness of the reflex threshold
for the whole nerve must have resulted both at A and at B from the
summation of the results of two component stimuli, each in itself sub-
liminal (as regards reflex effect), the one in the L division of the nerve
and the other in the M division. Such summation must be referable to
a subliminal central effect from L combining with a subliminal central
effect from M. Cutting half the nerve proximal to electrode A in the
first observation and proximal to B in the second reduced the number of
such excited afferent fibres and so necessitated an increase of stimulus
in order to excite fresh afferent fibres to replace those removed by the
section. Repetition of this experiment on another preparation gave
identical results.

DISCUSSION.

Experiments demonstrating spatial summation in occasional obser-
vations have been previously described (3, 5, 9); in the present investiga-
tion it has been found in almost every case whether the stimuli were
applied to the same nerve or to different nerves. Though no reflex was
produced by either stimulus alone, nerve impulses must have travelled
up some afferent fibres. This shows that in the spinal or decerebrate
flexor reflex a single impulse in a single afferent fibre is rarely, if ever, a

stimulus of more than subliminal value. Facilitation either spatial or temporal is necessary for reflex discharge. The design of the central nervous system is as favourable for spatial summation as the discharge of the receptor organs is for temporal summation. Where is the central locus of this process of summation of the excitatory effects of single impulses in single afferent fibres? Undoubtedly spatial summation must occur at the place of convergence of the afferent fibres on the final common path, *i.e.* at the synapse or in the neurone itself central to the axon hillock, and from its close similarity to spatial summation it is likely that temporal facilitation occurs at an identical place. When the propagated disturbance reaches the region where summa-tion can occur, it is not transmitted straight through, but is changed to an excitatory state which, if of sufficient intensity, sets up a fresh propagated disturbance, the reflex discharge. This requisite degree of excitation for initiating a discharge down the axis cylinder of the neurone can only be attained by the summation of the excitatory states produced by the arrival of several afferent impulses. Weak stimuli give rise to a threshold excitation in very few neurones, but have a considerable subliminal influence—the subliminal fringe. Strengthening of the stimulus adds to the excitation existing in these neurones, raising it to above the threshold value; fresh neurones are, however, added to the subliminal fringe. With strong stimuli practically all the neurones may be brought into the supra-liminal group, the subliminal fringe then ceasing to exist (*e.g.* peroneal nerve on spinal semitendinosus). It is the subliminal fringe which makes facilitation possible.

Reduced reflex time is probably mainly occupied in the time taken for excitation to attain neurone threshold. In the flexor reflex the response to a single stimulus is usually single because the rate of dis-appearance of the central excitatory state is so rapid. The same ex-planation accounts for the facility with which excitatory rhythms are transmitted as response rhythms. As yet we do not know the effect of a reflex discharge on the excitatory level of the neurone, but it seems likely that there will be exhaustion of some central excitatory state, a condition tending to prevent further discharges. The overlap of excita-tory afferents on any particular neurone and the power of summation is such that the accumulation of excitation may be great enough to cause several discharges—after discharge and secondary waves.

At first sight it seems difficult to reconcile our results with experi-ments[18] showing that, in the tetanic spinal flexor reflex, there is no

increase in the number of excited motor units with continuance of the stimulation (*d'emblée*). These results were obtained with strong stimulation at a comparatively slow rate (20σ between stimuli). With strong stimuli the subliminal fringe is relatively very small in comparison with the above-threshold excitations, hence the difficulty of detecting any minute amount of temporal facilitation which might occur. Reflex facilitation between two successive stimuli to the same afferent was found in isolated experiments by Forbes, Querido, Whitaker and Hurxthal[14], and an optimum interval of 15σ to 30σ was noticed. That they did not find it more often is perhaps to be attributed to their use of stimuli well above threshold. Others[28, 2] have failed to observe it for the same reason.

The significance of the various facilitation curves is by no means clear. Undoubtedly they are related to the values of central excitatory state at the indicated intervals. With tibialis anticus we have been able to explain the curves as complexes of two types of central excitatory state and to show that the delayed component is produced by the tension afferents of gastrocnemius-soleus, being probably of the nature of a rebound following an initial inhibition. Semitendinosus has displayed a certain uniform behaviour with any particular pair of afferents, and doubtless the facilitation curves obtained are compounded of the effects of central excitatory states with characteristic time processes. This complexity of central excitatory state following a single afferent volley was most unexpected. It is a striking illustration of the mixed character of afferent nerves[26, 27] and serves as a warning against too simple a conception of what has hitherto been regarded as an extremely simple type of reflex response—the ipsilateral spinal flexion reflex. Moreover it indicates the disadvantages of nerve stimulation in the study of reflexes, for under these conditions afferent fibres of the most diverse types are stimulated, and the central neurones are subjected to the simultaneous arrival of these propagated impulses—a circumstance far removed from physiological conditions.

SUMMARY.

The central condition produced by a single volley of afferent impulses in an ipsilateral flexor centre has been investigated by sampling with a second afferent volley (usually in another nerve) at various time intervals after the first. Under these conditions, when each reflex stimulus was just threshold, reflex responses were produced at certain stimulus intervals. This can be explained only by the effects of central summation.

Curves can be drawn in which the intervals between the stimuli are plotted against the tensions of the reflex responses.

With the twin nerves of gastrocnemius acting as afferents reflexly on tibialis anticus there is often an optimum degree of facilitation at simultaneity of the stimuli and also with the stimulus to one or the other nerve leading by an interval of about 12σ. This double effect was traced to two separable central excitatory states, one "direct," the other "delayed." Evidence is given that this second effect is evoked by the tension receptors of gastrocnemius, and is possibly a rebound following an initial inhibition. There is thus a complex central condition following a single afferent volley.

When semitendinosus was similarly excited from various nerve pairs complex curves were also obtained, but no attempt at analysis has been possible.

The most striking feature of the results has been the comparatively long duration of the central effect of one threshold stimulus as shown by its power of facilitating the effect of a second threshold stimulus. This shows that the first single afferent volley must produce an enduring central state—the central excitatory state—which is capable of summation. Moreover, since we find facilitation between threshold stimuli is almost universally demonstrable, it would seem that a single afferent impulse is by itself unable to produce a threshold central excitatory state in a neurone. Summation is necessary for every reflex discharge. Reflex threshold or neurone threshold is to be distinguished from afferent nerve threshold.

The enduring central excitatory state is responsible for after-discharge, an extreme example of which is described in a de-afferented tibialis anticus of a chronic spinal dog.

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