

CROSSED EXTENSOR REFLEXES AND THEIR INTERACTION.

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I. INTRODUCTION.

WHEREAS the "principle of convergence"⁽²¹⁾ of different spinal paths upon the motoneurons forming their "final common path" has been repeatedly studied on "antagonistic" reflexes (⁽²³⁾, p. 135), the same problem has received much less attention from the closely related aspect of "allied" reflexes (⁽²³⁾, p. 120) influencing each other. Earlier investigations by Sherrington⁽²²⁾ and Camis⁽⁵⁾ were recently extended by Cooper, Denny-Brown and Sherrington⁽⁸⁾, who, using a method similar to the one employed in this paper, and working with ipsilateral spinal flexor reflexes, analysed in detail the types of interaction met with. When the individual reflexes from any nerve pair were elicited in such a temporal combination that they overlapped, it was usually found that the resulting reflex contraction in the muscle investigated was less than the algebraic summation of the two reflex responses taken individually. The deficiency was shown to be due to a process which was designated occlusion, and which is really a manifestation of the "principle of convergence." Sometimes definite evidence of inhibition was met with, and, on comparatively rare occasions, one reflex seemed to be facilitated by the other. The full relevance of these conceptions will be explained later.

On account of the differences shown^(17, 18, 19) to exist between flexor and crossed extensor reflexes, it was considered important to carry out an investigation similar to the above, on the crossed extensor reflex.

II. METHOD.

The animal (cat) being deeply anæsthetised, deafferentation was performed; the 4th, 5th and 6th post-thoracic roots for quadriceps and the 6th, 7th, 8th and 9th for soleus and gastrocnemius⁽²⁰⁾. Decerebration (intercollicular) by the trephine method immediately followed. The anæsthetic was discontinued and the rest of the operation including the immobilisation, by appropriate nerve and tendon section, of every muscle.

except the one to be recorded from, and the denervation of the skin, was continued after an interval.

At first the whole quadriceps was recorded from, but for the most part only one or two of its component parts have been used because it was suspected that its component muscles did not behave in identical fashion, and this suspicion was later confirmed. The buried electrodes (9) were found successful in avoiding deterioration of the nerve stimulated.

Deafferentation, though adding to the severity of the operation, was thought necessary, to guard against excitatory and inhibitory influence (26), (16), (15) p. 436, and (11) arising from the proprioceptors of the contracting muscle itself.

Fixation for quadriceps has been secured by steel drills in both ends of the femur and a pelvic clamp, all of which have been rigidly attached to uprights clamped to the heavily weighted table on which the preparation rests. For soleus it is necessary to drill the tibia at both ends, and for gastrocnemius the femur in addition has to be similarly fixated. Care has been taken to give the muscle free play by isolating it from surrounding fascia and muscles, and in a groove in the piece of bone which has been cut out at its insertion, rests the steel hook which connects it to the lever arm of the high frequency isometric optical myograph which has been used throughout this investigation. The more recent work has been done with the improved mirror myograph (10) which has enabled us to record from two muscles simultaneously. Especial care has then to be taken to adjust the initial tension of each muscle to a comparable amount and a complete separation of the two muscles is essential.

Time has been recorded by a Rayleigh magnetic wheel. Stimulation has been by coreless Berne coils delivering about 50 double shocks per sec. with two volts in the primary. (With the double myograph 90 double shocks per sec. were used.) The signals have been worked by the camera and the shadow of the short-circuiting key of the secondary has been thrown on the camera slit by the same source of light as was used for the myograph.

Owing to the influence of the labyrinthine and neck reflexes (1) on the reflex centres of the cord, care has been taken to keep the head in a fixed position during a series of observations. It has generally been in "minimal" position and the animal has rested on the side opposite to the muscle which is being recorded from. The temperature has been taken deep in the inguinal wound at intervals during the experiments, and, as a rule, has been kept fairly steady about 36° C. Variations of 2 degrees from this were rare.

As a rule no observations have been made until at least 4 hours have elapsed after the cessation of the anaesthetic. Even then it has generally been observed that the crossed extensor response has increased steadily during the experiment even for as long as 10 hours after the operation.

When studying interaction we have usually combined the two reflexes in question in overlapping or intercurrent sequence, but sometimes both have commenced almost simultaneously. Control observations of each individual reflex are important as inconstancy is frequent. All unreliable observations have been discarded. The agreement of controls was often not so absolute as is shown in the diagrams, but in these and other cases from which data have been derived, the variations are so slight as to be

negligible. All the figures except Fig. 1 are tracings from the negatives of the photographic records.

III. RESULTS.

1. *Crossed extensor reflexes.*

The main features of this type of reflex (23), (26) and its reciprocal relationship (24), (27), (28) have already been described. Graham Brown(3) has given an account of the crossed extensor reflex and its numerous variations as it is seen in the gastrocnemius-soleus muscle. More recently Liddell and Sherrington (17), (18), (19) have described in detail the differences existing between the crossed extensor reflex and the flexor reflex. In the former temporal summation plays an important part revealed by progressive involvement of fresh motor units, "recruitment," and after-discharge is a marked feature in the undeafferented preparation(26). Fulton and Liddell(16) have produced evidence showing that recruitment was to a large extent produced by "auto-genous" inhibition arising from the muscle's own contraction. Denny-Brown(11) has proved the presence of this inhibition.

Gastrocnemius has been an unsatisfactory muscle as its response even to strong stimulation of crossed nerves is usually very small. In this we confirm Denny-Brown(12). We will confine our attention to soleus and various component muscles of quadriceps.

Latent period has been of very variable duration. The individual makes and breaks of the primary were not photographed, so that, as the unshortcircuiting signal has to be used as the basis of measurement, an error of several sigmata was always possible. This error was often minimised by taking the shortest latency of a series. In the deafferented quadriceps the latent period is, as a rule, longer than in the undeafferented quadriceps in which latencies shorter than 40σ were common, and in one case a latency of 22σ was observed. 40σ has been the shortest latency which we have recorded in the deafferented preparation, but values between 40 and 50σ have been common. With soleus muscle latencies have been somewhat longer and values less than 60σ have been rare. It has been impossible to establish any regular relationship between the length of the latent period and the nerve stimulated. Weakening the reflex has invariably lengthened the latent period(18), and latencies up to 500σ have been observed.

Recruitment. As a rule in the deafferented preparation the long gradual rise described by Liddell and Sherrington(18) for the undeafferented preparation has been a rare feature, and at times the reflexes

have been almost "d'emblée" in character. Where control motor tetani have been elicited by stimulation of the motor nerve we may obtain some idea of how closely the crossed extensor reflex sometimes approximates to the motor tetanus. As a standard of measurement in any particular case we have used the time from the first sign of contraction to the attainment of 90 p.c. of the total tension developed in that case.

In the experiment quoted below all the stimulations were maximal and, in all, the reflex responses were at least 50 p.c. of the motor tetanus. Both muscles were recorded from simultaneously.

Muscle	Motor tetanus	Peroneal* nerve	Post-tibial* nerve	Quadriceps* nerve
Vastus medialis	160 σ	230 σ	200 σ	260 σ
Vastus lateralis	120 σ	230 σ	210 σ	280 σ

* Only the effects of stimulating nerves of the hind limb opposite to that of the registering muscle are considered in this paper.

In these cases the total period of recruitment must be practically over in 200 σ and the greater part of it has occurred within a period of 100 σ from the earliest reflex response. When peroneal and post-tibial nerves were stimulated simultaneously, vastus medialis developed 90 p.c. of the total tension in 170 σ . In this case the reflex discharge of all the motoneurons was almost simultaneous. In Fig. 7 are further examples of rapid recruitment.

Soleus generally shows a more gradual recruitment.

This is shown in Fig. 6 C, though the soleus in this case is particularly rapid, for a motor tetanus reaches 90 p.c. of its total tension in 195 σ (260 to 290 σ are more normal figures in our experience). The maximum reflex responses to internal saphenous and post-tibial nerves take 420 and 480 σ respectively. With weaker reflexes there is but little increase in this period (Fig. 6 A and B).

Contrary to the finding of Fulton and Liddell(16) we have occasionally found the two-stepped ascent in the deafferented preparation. In these cases, however, there was always other evidence, especially rebound, of the presence of inhibition.

After-discharge. With deafferented quadriceps after-discharge at plateau height usually continued for 100 to 200 σ for reflexes of 1 to 1½ sec. duration and then the tension dropped abruptly. With motor tetani of similar duration the time from the cessation of the stimulus to the angle was 35 to 40 σ . In those cases where the reflex was falling away before the cessation of the stimulus a more abrupt falling away commenced often at much less than 100 σ . With soleus where the terminal mechanical response of the motor tetanus has been about 80 to 90 σ , the after-discharge is also usually longer, often much greater than 200 σ .

When the preparation has been in bad condition there has been an enormous prolongation of after-discharge, the return to resting tension often taking as long as a minute. This is not a contracture due to fatigue of the peripheral mechanism (2), for motor tetani were normal.

Fractionation of quadriceps. With a double myograph vastus medialis and vastus lateralis have been used together. There was a striking similarity in the responses of the two muscles (Fig. 9), though closer analysis has revealed a small but constant difference between them. Fig. 1, where the maximum reflex tetanic responses of both, simultaneously

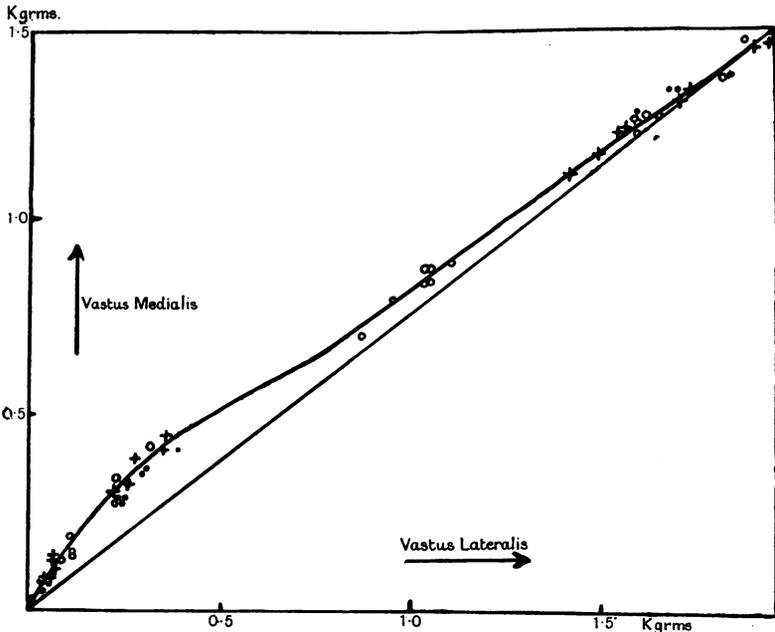


Fig. 1. Graph of simultaneous tension development in vastus medialis (ordinates) and vastus lateralis (abscissæ) (both deafferented). Crosses responses to superficial peroneal nerve, dots to post-tibial nerve, and circles to stimulation of both simultaneously.

recorded, are plotted against each other, shows the remarkable constancy of their relative contractions. Strong reflexes were interspersed with the weak so that no gradual change the preparation was undergoing would affect the results. Though some intermediate values are missing it is obvious that with weaker reflexes vastus medialis tends to predominate, but near threshold it falls off more rapidly than does vastus lateralis so that their thresholds were the same. The responses to post-tibial nerve

and to superficial peroneal nerve lie on the same curve. The predominating response of vastus lateralis in strong reflexes is attributable to its greater size and not to a greater proportion of its motor units being excited.

Rectus femoris and vastus medialis as a pair show less similarity (Fig. 2). Threshold has been distinctly lower for vastus medialis, and

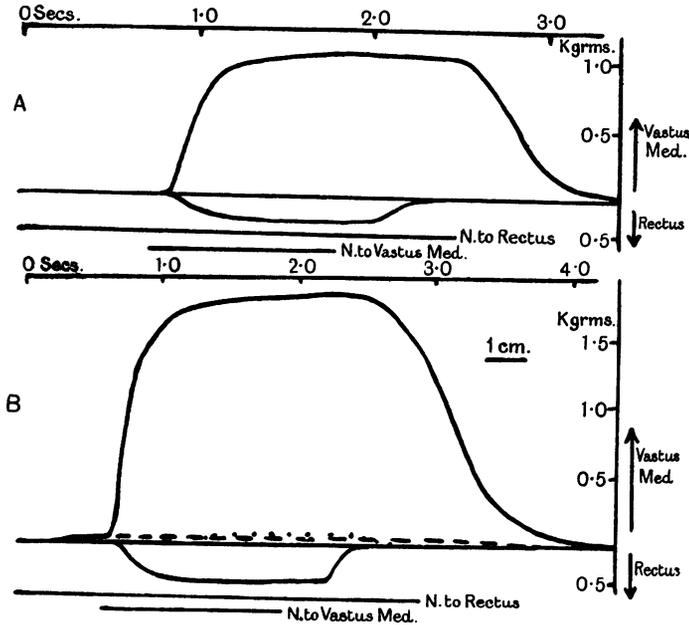


Fig. 2. A. Stimulation of crossed nerve to rectus (12 cm. coil) with intercurrent stimulation of crossed nerve to vastus medialis (14 cm. coil). No contraction of either muscle to either nerve stimulated independently. Both muscles deafferented. Magnif. = 550. Lines below curves show duration of stimuli. Time is recorded on line above and tension on line to right side.

B. As above but strengths stimulation increased to 11 cm. coil for nerve to rectus and 13 cm. coil for nerve to vastus medialis. Each alone causes a small contraction in vastus medialis as is shown by dashes for nerve to rectus and by dots for nerve to vastus medialis. Rectus muscle still does not respond to either nerve stimulated independently.

with weak reflexes the latent period has been longer for rectus, but for strong reflexes the latent periods of both muscles have been approximately equal. In rectus there has been more abrupt tension development, plateau after-discharge is shorter and the decline of tension much more rapid. Sustained facilitation (see later) though present is much less prominent in the reactions of rectus than it is with vastus medialis (Fig. 2). Decline of response of rectus has occurred simultaneously with

increase in vastus medialis. Marked rebound has been observable in rectus with none, or only a trace, in vastus medialis. Sometimes in the interaction of two reflexes occlusion has occurred in vastus medialis simultaneously with facilitation in rectus. Such findings as these emphasise the importance of recording from only one component of quadriceps at a time.

There is, therefore, a certain selective excitation of the motoneurones of the whole quadriceps centre according to which component muscle they belong. With vastus medialis and vastus lateralis this is slight, and it is highly probable that a large number of afferent nerve fibres are "proper" to both muscles(7). The remarkable relative constancy of the responses of these two muscles seems incapable of explanation in any other way. The much more distinctive behaviour of the motoneurones of rectus is not surprising, because rectus, being a double joint muscle, is a potential flexor of the hip as well as an extensor of the knee. Though it probably never acts in the former capacity, reflexes calling it into activity have also to fixate the hip to prevent flexion there. One would therefore expect its motoneurones to be for the most part "proper" to afferents which do not include the motoneurones of the rest of the quadriceps in their reflex "field."

2. *Interaction of crossed extensor reflexes.*

The features evident in interaction between two crossed extensor reflexes can be considered under the same headings used for the ipsilateral spinal flexor reflexes(8).

(i) Two reflexes when combined produce more tension in the muscle than summation of their individual effects—facilitation.

(ii) Two reflexes with little or no evidence of possessing inhibitory components give, when combined, less tension development in the muscle than summation of the results of each singly—occlusion.

(iii) More complex phenomena exhibited by reflexes showing marked inhibitory components.

The tension developed by the muscle has been used as a measure of number of motor units excited. Denny-Brown(12) has shown this to be approximately correct.

(i) *Facilitation.*

A. In *concurrent facilitation* the effect is exerted by one reflex on another simultaneously excited. We have found that concurrent facilitation is more easily and regularly obtained in the crossed extensor reflex

than was found to be the case with the flexor reflex (8), but it has been rather rare to find that two reflexes, themselves subliminal, are capable of evoking a marked reflex response when concurrent.

Thus, neither post-tibial nerve nor superficial peroneal nerve caused any response in crossed deafferented soleus when stimulated independently, but when concurrent evoked reflex contractions of 90 and 110 gm. on two successive occasions. The crossed nerve to vastus medialis, and the crossed nerve to rectus, stimulated independently, repeatedly produced no reflex response. When stimulated concurrently a large contraction in both rectus femoris and vastus medialis was regularly produced, e.g. 1.1 kg. in vastus medialis and 0.35 kg. in rectus (Fig. 2 A).

Somewhat similarly when the stimulation of one nerve alone is inefficient, when intercurrent it facilitates a weak reflex from another nerve (Fig. 3 B), or, inversely, if the weak reflex is intercurrent in

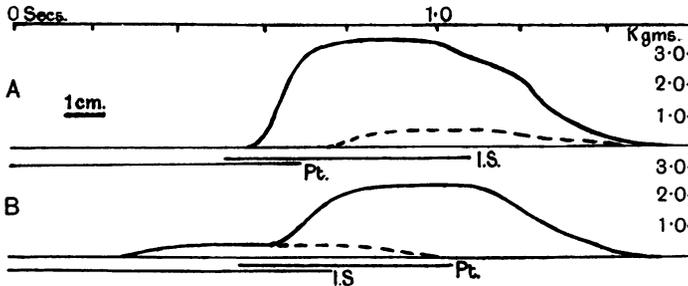


Fig. 3. A. Stimulation of crossed popliteal (*Pt.*) and internal saphenous (*I.S.*) nerves in overlapping sequence. Popliteal alone (16 cm. coil) was just below threshold. Internal saphenous alone (15.5 cm. coil) produced a small response as shown by dotted line. Muscle-rectus with vastus lateralis (deafferented).

B. As above, but stimulations overlap in reverse sequence.

the non-effective stimulation, the weak reflex is markedly facilitated (Fig. 3 A).

Thus crossed nerve to vastus medialis caused a small reflex response of about 50 gm. in the vastus medialis muscle and nothing in rectus. Independently the crossed nerve to rectus had no reflex effect on either muscle, but, when intercurrent in the weak reflex from nerve to vastus medialis, it caused an abrupt tension development of 2.5 kg. in vastus medialis and 1.4 kg. in rectus.

Facilitation has been commonest between weak reflexes.

Thus (Fig. 6 A) soleus develops 320 gm. with post-tibial nerve alone and 480 gm. with internal saphenous nerve. When both are stimulated together 950 gm. tension is produced. Again with soleus 70 gm. from superficial peroneal nerve and 180 gm. from post-tibial give 300 gm. when concurrent. With vastus medialis 0.40 kg. from small sciatic alone, and 1.25 kg. from one plantar facilitate to give 2.37 kg. when combined, and again with vastus medialis. (Fig. 4 A) 0.16 kg. from one plantar and 0.22 kg. from the other give 0.63 kg. when combined.

Facilitation is particularly frequent and sometimes extreme between afferent nerve pairs closely allied in distribution, *e.g.* two nerve branches to quadriceps, or two plantar nerves.

Facilitation invariably shortens the latency of the response to the

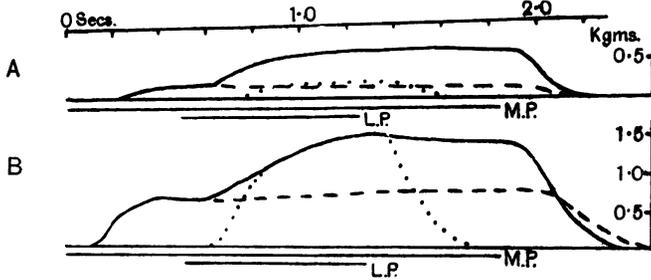


Fig. 4. A. Lateral plantar nerve stimulus (L.P., 30 cm. coil) intercurrent in medial plantar nerve (M.P., 28 cm. coil). Contraction to M.P. alone is shown by dashes, and to L.P. alone by dots.

B. As above, but strengths of both lateral and medial plantar stimuli increased to 26 cm. coil distance. Deafferented vastus medialis. Magnif. = 550.

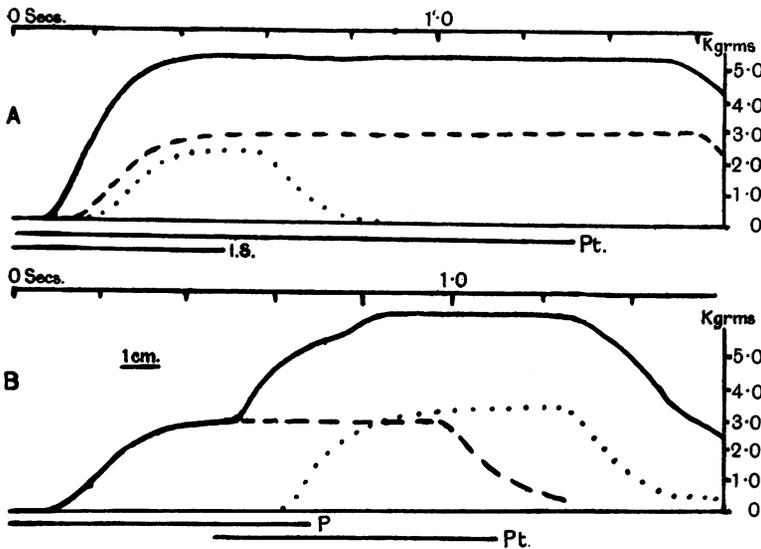


Fig. 5. A. Deafferented vastus lateralis and rectus, stimuli to internal saphenous nerve (I.S., coil 10 cm.) and popliteal nerve (Pt., coil 14 cm.). Control reflexes: dashes for Pt. and dots for I.S.

B. Same muscle and preparation as above. Stimulations applied to peroneal nerve (P., coil 13 cm.) and popliteal (Pt., coil 16 cm.). Dashes show peroneal reflex alone and dots popliteal reflex alone.

intercurrent stimulus, or, if both stimuli commence almost simultaneously, the combined response commences earlier than with either individually.

Thus (Fig. 4 A) the latent period of the intercurrent plantar is 220σ when alone and 70σ when intercurrent. Fig. 2 B is an extreme example as the latency of the response to stimulation of the nerve to vastus medialis is 400σ when alone and only 40σ when intercurrent in a weak response to nerve to rectus. Fig. 3 A is also a striking example. In Fig. 8 A where the facilitation is of a less degree the latent period of the small sciatic response is 170σ when alone and 135σ when intercurrent. Fig. 5 A and B are marked examples of shortening of latent period with only a small degree of facilitation. Thus (Fig. 5 B) the popliteal reflex has a latency of 94σ when alone and 44σ when intercurrent in a peroneal nerve response.

The degree of facilitation of a short intercurrent reflex of constant length varies according to its time of occurrence relative to a constant long continued reflex.

Thus superficial peroneal nerve was stimulated intercurrently for 0.58 sec. at various periods relative to a post-tibial nerve stimulation lasting 2.34 sec. The two muscles registered simultaneously and the maximum tensions developed are tabulated below. Both nerves were in fluid electrodes and the strength of stimulation was at $16\frac{1}{2}$ cm. coil distance which was just above threshold, a condition necessary for the occurrence of facilitation.

Temporal order of observation	Interval between commencement of post-tibial and beginning of superficial peroneal nerve stimulation	Vastus medialis tension in grm.	Vastus lateralis tension in grm.
7	Simultaneous	340	230
1	100σ	420	320
4	160σ	280	230
5	230σ	150	115
6	360σ	150	115
2	760σ	190	120
3	1580σ	130	90

During this series of observations repeated controls were taken of the responses elicited from each nerve singly, and a fair constancy was observed with, however, a noticeable falling off towards the end of the series. This doubtless accounts for the high value of the observations with 760σ and the comparatively low value obtained with both reflexes commencing simultaneously. The average values for superficial peroneal nerve alone were 100 and 75 grm. for vastus medialis and vastus lateralis respectively, and for post-tibial, nerve alone 55 and 40 grm. The background reflex (post-tibial) definitely showed falling away after 600σ and the explanation of the lessened facilitation occurring when the superficial peroneal was intercurrent after this period is certainly due to this so-called "fatigue" of early onset. What its nature is we do not know (*vide infra*, p. 116), but it seems that it can be demonstrated by a lessening of the facilitating power of a reflex long before any falling away of the already existent contraction is apparent, e.g. facilitation at 230σ interval is definitely less than at 160σ though falling away was not evident till 600σ .

This curious diminution of facilitating power in the latter parts of a reflex response was also shown by the effect of an intercurrent break shock to a crossed nerve. Alone a shock to internal saphenous nerve produced a 20 grm. contraction in soleus, but, when intercurrent in a reflex from post-tibial 0.77 sec. from its commencement (plateau had just been reached), there was a tension increase from 340 to 510 grm. When the same shock was 1.75 sec.

from the commencement of the background reflex, then the tension increase was only from 320 to 360 grm. This reflex background had shown no signs of falling away and yet this marked diminution of its facilitating power had occurred.

In Fig. 6 *B* a very early intercurrent stimulus produces less extra tension rise than one occurring later. Similar results have also been

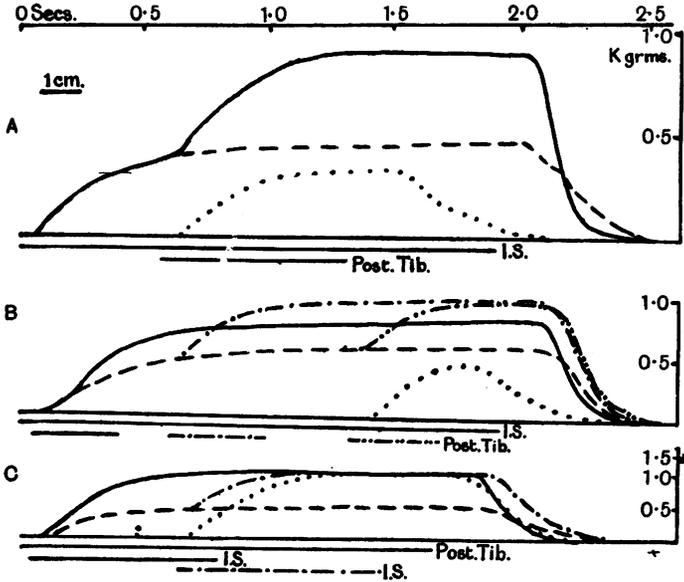


Fig. 6. *A*. Deafferented soleus post-tibial nerve (coil 20 cm.) intercurrent in an internal saphenous nerve stimulation (coil 33 cm.). Dashes show internal saphenous alone, and dots post-tibial alone.

B. Muscle and nerves as above and same strengths stimuli to both. As shown by lower signal lines post-tibial stimulus incident at various points in reflex background of internal saphenous. Continuous line reflex corresponds to the continuous line signal for post-tibial nerve. The dot dash line corresponds to the dot dash signal and the double dot dash line to the double dot dash signal. Corresponding to this latter is control of post-tibial reflex alone. Dashes show the control of internal saphenous alone.

C. Muscle as above. Post-tibial at 16 cm. coil with internal saphenous at 20 cm. coil intercurrent at two different times. The dashed line is post-tibial reflex alone, and dotted line internal saphenous reflex alone.

obtained with early intercurrent break shocks. They are most often observed with the comparatively slow recruiting reflexes of soleus as backgrounds. It seems that the facilitating power of a reflex is not maximal until recruitment is almost complete. These two factors of "fatigue" and recruitment are opposed to each other, and the point of

optimal facilitation seems to be after recruitment is practically complete and before "fatigue" has advanced very far.

B. In *sustained facilitation* the facilitation has appeared as an after-effect of one reflex on the other. This has been a very constant and striking feature in our investigations on the crossed extensor reflex (both when the interacting reflexes have occluded and facilitated each other). This is in marked contrast to the ipsilateral spinal reflex (⁽⁸⁾ p. 291) where it was unusual for the reflex which emerged from the occlusion to have suffered any marked changes, but it appears more common when the intercurrent stimulus is a single break shock (13).

In Fig. 5A popliteal, which alone develops only 2300 grm., maintains perfectly for 1 sec. a plateau height of 6100 grm. which is developed initially by a short concurrent internal saphenous stimulation. In Fig. 6 is a similar phenomenon seen in soleus. Figs. 4A and B show sustained facilitation both with occlusion of strong reflexes and facilitation of weak reflexes. See also Figs. 5B and 8.

How long can the effects of the concurrent reflex be manifest in the reflex emerging from the concurrence? The duration is very variable, as can be seen in some cases where the falling away commences almost as early as it would with the intercurrent reflex alone. Especially interesting are those cases where facilitation occurs between two stimulations which alone give no reflex response.

Thus with crossed nerves to rectus and vastus medialis as afferents the reflex contraction in vastus medialis produced by concurrent facilitation is maintained by nerve to rectus alone for 630σ. However there is less "central drive," for after-discharge (at plateau height) is then only 160σ when stimulation of nerve to rectus ceases, whereas when stimulation of nerve to vastus medialis ceases only 75σ before that of nerve to rectus, the after-discharge at plateau height is 260σ. With longer continuance of stimulation of nerve to rectus after concurrence it was found that tension only fell from 0.68 kg. to 0.62 kg. in 1.6 sec., and it took 4.8 sec. for the sustained facilitation to completely disappear.

Again, with soleus (deafferented) the concurrent stimulations to post-tibial nerve and to internal saphenous nerve developed a plateau tension of 1.05 kg. On cessation of the stimulus to internal saphenous, which alone developed 0.90 kg., there was no fall in plateau height for 1.6 sec., and, when the stimulus of post-tibial nerve was finally discontinued 1.82 sec. later, the tension had only fallen to 0.77 kg., though post-tibial nerve alone was only capable of developing a tension of 0.66 kg. Here a considerable facilitation had persisted for 3.42 sec.

In the crossed extensor reflex sustained facilitation has been demonstrable with all nerve pairs and muscles used, exceptions being of course complete occlusion of the precurrent or intercurrent reflex and also when

one reflex markedly inhibits the other. From the foregoing account it is obvious that the phenomenon is allied to after-discharge. The only other possible suggestion would be an effect of the nature of rebound due to some underlying inhibition. In the cases discussed there has, however, been no evidence whatever of any marked inhibitory factor. Moreover, it is hardly likely that rebound should exactly and precisely equal the amount of the additional contraction due to the concurrence.

(ii) *Occlusion.*

We have found occlusion between reflexes excited from even the most diverse nerve pairs. Its amount has been estimated by observing the percentage deficiency of a reflex contraction when intercurrent, taking as standard the reflex contraction elicited alone. It is recognised that this is a purely arbitrary value as it assumes that all the occlusion has occurred at the expense of the intercurrent reflex, a totally different value being obtained if the reflex sequence is reversed (8). No account is taken of simultaneous facilitation which doubtless often occurs, and which would tend to make the amount of occlusion appear smaller than it actually is.

In agreement with findings on the ipsilateral spinal flexion reflex (8) we have found in the crossed extensor reflex:

1. Those afferent nerves which produce the largest reflex responses are as a rule the most powerful occluders. Thus popliteal or post-tibial nerves which evoke large reflex responses in quadriceps, or its component muscles, are powerful occluders.

2. As the individual reflex responses from any particular nerve pair increase (due to increase in strength of stimulus), the degree of occlusion between them increases.

3. The degree of occlusion decreases in those cases where the reflex background falls away.

4. Other things equal, the degree of occlusion is greater between afferents having a closely allied peripheral distribution, *e.g.* plantar nerves.

Our findings for the crossed extensor reflex have, however, differed from those for the ipsilateral flexor reflex (8) in that we have found that the amount of occlusion was dependent on the temporal position of the intercurrent reflex relative to the background reflex.

Thus in Fig. 7 *A* when the internal saphenous response is intercurrent in the post-tibial response it is practically totally occluded. When both stimulations commence together there is much less occlusion (Fig. 7 *B*), and this lessened degree of occlusion is maintained throughout the reflex. Again for vasto-crureus, a peroneal stimulus when intercurrent was

completely occluded by popliteal, but, when both commenced together, there was only 70 p.c. occlusion.

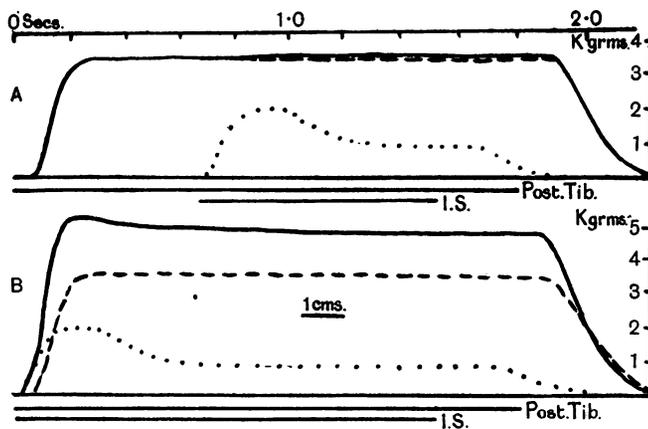


Fig. 7. *A.* Deafferented vastus lateralis. Internal saphenous nerve stimulation (coil 10 cm.) intercurrent in post-tibial nerve stimulation (coil 13 cm.). Dotted line shows control of internal saphenous alone, and dashes post-tibial alone.

B. As above but internal saphenous stimulation begins simultaneously with post-tibial. Controls shown as above.

A similar feature has already been described when dealing with facilitation and it seems likely that in this case the variation in amount of occlusion is only apparent, the real cause being the increased facilitation simultaneously occurring when the intercurrent reflex is early.

The latent period of the increase in tension produced by an intercurrent reflex has not borne a constant relation to the latent period of that reflex when elicited independently. Thus in Fig. 4 *B* the latent period of the lateral plantar undergoes no detectable change when it is intercurrent, both latencies being about 80σ . Again the latent period of peroneal is lengthened from 48σ when alone to 136σ when following on a popliteal reflex. Again in Fig. 8 *B* the latency of the response to small sciatic is increased from its independent value of 90σ to 170σ when it is intercurrent. This case is particularly interesting because when both stimuli were weak a shortening of latent period had occurred (Fig. 8 *A*), as already mentioned under facilitation. It seems that two different processes are involved. In Fig. 8 *A* there is an earlier response to the small sciatic stimulus when intercurrent, because certain neurones have been subliminally excited by the plantar nerve stimulus and so are partly prepared to respond to the small sciatic. In Fig. 8 *B* where almost total occlusion occurs this facilitation is not present, and, moreover, all the

low threshold neurones of small sciatic which would soon recruit over the threshold are already excited. The latent period is therefore necessarily

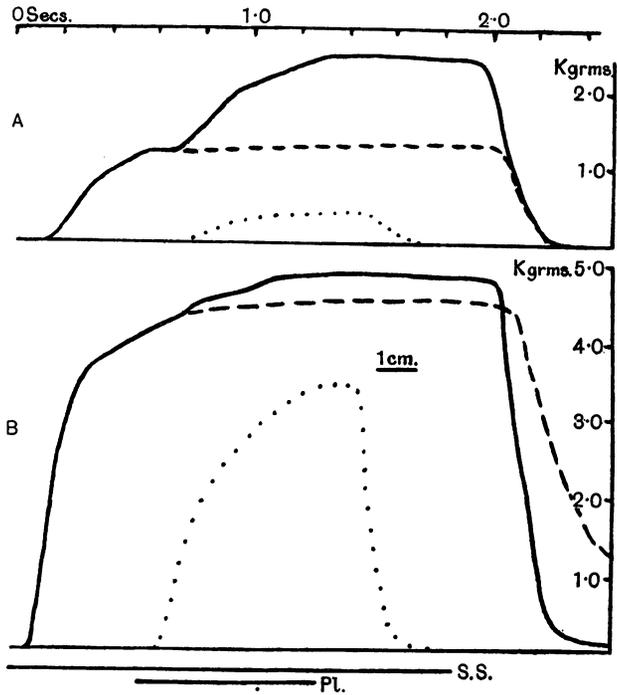


Fig. 8. A. Deafferented vastus medialis. Small sciatic nerve (*S.S.*) intercurrent in plantar nerve (*Pl.*). Both coils 26 cm. Control of small sciatic alone shown by dotted line and plantar by dashes. Signals shown below B.

B. As above but strength increased to 18 cm. coil for small sciatic and 16 cm. for plantar nerve. Magnif. = 550.

prolonged till the few non-occluded high threshold motoneurones attain threshold value.

It has been difficult to get definite evidence on the effect of concurrence on the rate of recruitment. A large number of reflexes were almost "d'emblée" in type and so for that reason little effect would be expected (Fig. 7 B), but even in these cases it has sometimes been possible to demonstrate an increase (*vide supra*, p. 100). With more gradual recruitment there has not seemed any marked effect of one reflex on the other. But in all our cases of gradual recruiting ascent there was evidence of inhibition as shown by rebound. This inhibition doubtless interfered with the summational process.

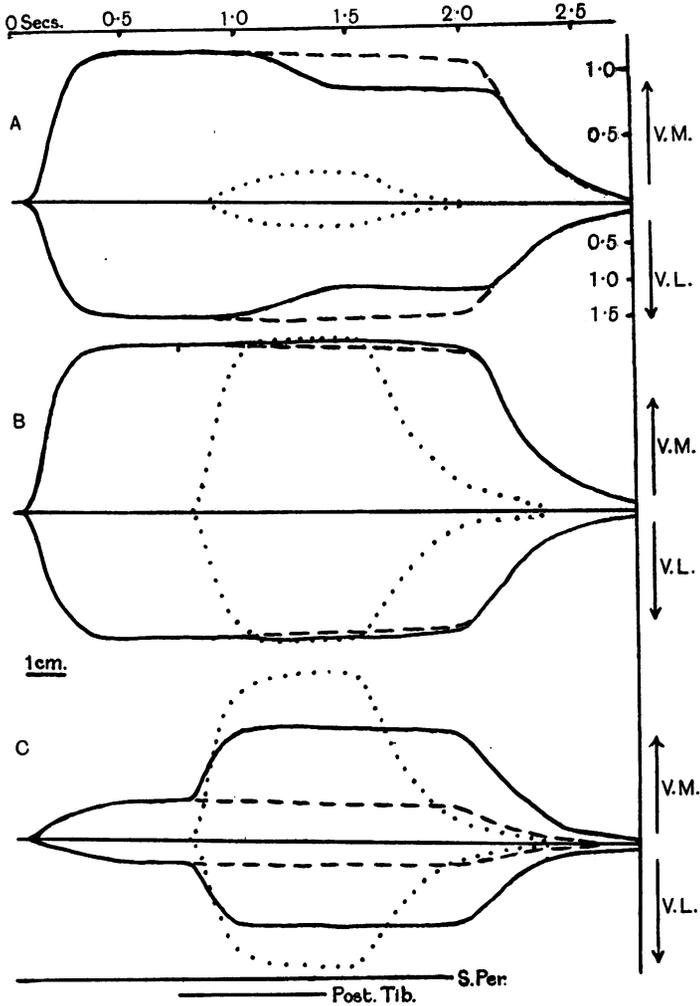


Fig. 9. Contractions produced simultaneously in deafferented vastus lateralis and vastus medialis by a crossed post-tibial nerve stimulation intercurrent in a crossed superficial peroneal nerve stimulation (*S. Per.*).

In *A*, coil for superficial peroneal nerve is on 14 cm. and for post-tibial nerve on 16 cm.

In *B*, coils for both nerves are on 14 cm.

In *C*, coil for superficial peroneal nerve is on 16 cm. and coil for post-tibial nerve is on 14 cm. In all controls of superficial peroneal nerve are shown by dashes and post-tibial nerve by dotted lines. The time and tension scales are identical for all. As shown by arrows at side, vastus medialis pulls upwards from a central zero line and vastus lateralis pulls downwards. Magnif. = 550.

When the intercurrent reflex is totally occluded, it is sometimes possible to see a definite prolongation of after-discharge of the background reflex.

Thus a peroneal reflex was completely occluded by a popliteal reflex, but the plateau after-discharge of the latter was then 182 and 190 σ on two successive occasions, whereas a control of popliteal alone taken between these two observations possessed only 140 σ plateau after-discharge. In other cases no such increase in after-discharge is present (Figs. 7 A, 9 B). In these cases, particularly in Fig. 9 B (see section on inhibition), inhibition is probably responsible for the absence of this lengthening.

(iii) *More complex effects exhibited by reflexes possessing both excitatory and inhibitory components.*

Crossed inhibition has often been associated with crossed excitation especially with internal saphenous or peroneal nerves. Increase of the strength of stimulus often greatly increases this inhibition. Even though inhibition be not apparent in the reflex when elicited singly it is often obvious in intercurrent (Fig. 9 A) or precurent combinations with another crossed extensor reflex, e.g. in Fig. 5 B, when the precurent stimulus to peroneal nerve ceases, there is a further rise in tension due to cessation of the inhibitory influence exerted by peroneal on some motor units. Rebound probably plays some part in producing this increased contraction, but it, too, is evidence of preceding inhibition (25), (14). Inhibition may also manifest its presence by reduction of an intercurrent test reflex (Fig. 9 C).

For the ipsilateral spinal reflex it has been conclusively shown that occlusion is a process distinct from inhibition though this may also be present (8). In the crossed extensor reflex inhibition has been a more common factor, so that the amount of true occlusion has often been difficult to estimate. Thus in Fig. 9 B the tension developed by post-tibial nerve alone is, if anything, slightly more than that produced by it when intercurrent in a superficial peroneal nerve reflex. We see from Fig. 9 C that a weak superficial peroneal definitely inhibits a post-tibial reflex of the same strength as above. It is obvious that in Fig. 9 B this inhibition must be present, but it is masked by the stronger excitation of superficial peroneal which almost exactly balances the inhibition, so that the tension developed by post-tibial when alone is practically equal to the total tension when it is intercurrent. We do not know whether this obliteration of inhibition under additional excitation takes place in those motor units which previously were inhibited or whether it is merely masked by the additional excitation of other motor units by superficial peroneal. Possibly both processes are partly concerned.

IV. DISCUSSION.

We have seen that facilitation can occur between two stimuli which alone give no reflex response. Spread of stimulus can be excluded. Although no reflex response was produced, some afferent fibres in both nerves must have been excited. Moreover, for facilitation to be possible, some at least of the excited afferents must converge on the same neurone, be it the motoneurone of the extensor muscle in question or an internuncial neurone. The morphological basis of an extensive overlap has been demonstrated by Cajal⁽⁴⁾ and others, and its physiological proof has been given⁽⁷⁾ for the flexor reflex, and for the crossed extensor reflex by us. From our knowledge of the structure of the neurone it is evident that the actual locus of the facilitation must exist somewhere between the termination of the afferent fibre on the surface of the neurone "boutons terminaux" and the axon hillock (⁽²⁹⁾ p. 524). The subliminal (in the sense that it is insufficient to evoke a discharge down the axis cylinder of the neurone in question) excitation produced by a series of impulses arriving at the endings of one afferent must be able to reinforce the subliminal excitation produced from the other afferent, with the result that a discharge down the axis cylinder of the neurone in question is now produced. This argument is independent of any theory of excitation. Concurrent facilitation must therefore depend on the excitation of two afferent fibres both of them proper to each neurone facilitated. It is significant that it is especially easy to obtain facilitation between closely allied afferents, and that the overlap existing between them in the reflex centre is large, as shown by their powerful occlusion when stimulated strongly.

When one or both of the component stimulations independently produces a reflex response, the explanation of facilitation is exactly as above with, in addition, the possibility in the latter case of the existence of occlusion between some of the excited motor units. This would have the effect of making the facilitation appear less than it really was. Doubtless facilitation occurs in many cases where we have no evidence of its existence—being masked by simultaneous occlusion or inhibition.

The latent period of a reflex has been shortened when facilitation has occurred. It might be argued that this is due to the earlier response of the motor units added by facilitation, and that those which are excited by the stimulus in question independently, suffer no such abbreviation of latent period. Where (Fig. 5 *A* and *B*), despite but a small facilitation, there is a great shortening of latent period, it seems certain that many of the independently excited motor units are responding earlier. Latent

period especially as seen in the weak crossed extensor reflexes is more correctly spoken of as "summation period" (6). Its shortening by a concurrent stimulation of another afferent can, on the same reasoning as above, be explicable only by the excitatory impulses from this afferent being also incident on the same neurone. There the excitatory processes from each afferent must reinforce each other so as to cause an earlier discharge of impulses down the axon of this neurone.

With "sustained facilitation" it is also simplest to consider first those cases where neither stimulus alone causes any reflex response. Concurrent facilitation occurs, and it is found, when one stimulus is stopped, that there is no abrupt cessation or decrease of the contraction. In any particular neurone the reinforcing action of one subliminal excitation on the other does not cease when the arrival of impulses from its afferent has terminated. It is difficult to think that "delay paths" can be considered when the duration of the after-action is as long as 5 sec. The excitation of the neurone from one afferent is now able to maintain its supraliminal excitatory state owing to the effect of the previously excited other afferent. There has been a "surcharging" of the neurone during the concurrence. One is driven to the conception of Sherrington⁽²⁹⁾ that there is an accumulation of a substance *E*, be it ions or a chemical substance, at some locus in the neurone. During concurrence of stimulation this mounts up above threshold. If both stimuli stop simultaneously, then the excess is able to maintain excitation for some time (after-discharge). If, however, only one stimulus ceases, then the other is continually adding more *E*. This rate of addition of *E* is alone unable to reach threshold, but, when starting with a "surcharge" of *E*, it is able to considerably retard the falling of this below threshold. After-discharge is produced by supraliminal excitation of neurones persisting after the actual stimulus has ceased. The persisting excitation evident in sustained facilitation is not present as after-discharge when one of the facilitating reflexes is evoked alone. The after-discharge, in that case, soon ceases for the excitation of each neurone rapidly drops below threshold. Sustained facilitation must be the manifestation of that enduring subliminal excitation, which, by summing with the subliminal excitation of the same neurones by the background reflex, is able to maintain a supraliminal excitatory state in those neurones. Sustained facilitation is therefore, for the most part, an index of subliminal after-discharge. Its long duration is therefore easily intelligible.

A remarkable feature is that very often after one stimulus has ceased some considerable time elapses before any fall in tension occurs. *A priori*, with both stimuli acting concurrently all grades of supraliminal excitation

would be expected, some neurones being just above threshold. In these one would anticipate that the cessation of one stimulus would immediately result in the excitation falling below threshold. That this is very frequently not the case seems to indicate that the neurone itself has "inertia." It seems likely that, once the supraliminal excitatory state is set up, the neurone continues discharging down its axon even when its excitation has fallen below the initial threshold value. The frequency of plateau after-discharge in crossed extensor reflexes (deafferented) is of course also evidence in favour of this.

In an example already given under sustained facilitation it was shown how the "central drive" of a reflex, as measured by duration of plateau after-discharge, diminishes when one stimulus alone keeps up the reflex tension developed by two. One had therefore been sustaining excitation in all neurones at the expense of the surcharge accumulated during concurrence.

A constant test stimulus to one nerve evoked a much larger reflex response when preceded, at a constant interval, by a longer than when preceded by a shorter reflex evoked from another nerve. More excitatory charge had accumulated during the longer stimulation of the preceding nerve, and this had facilitated the after-coming test response. Moreover, the after-discharge of this was also augmented, showing that the central charge had been stored all this time.

It was shown that the facilitating power of a reflex first increased till the tension had about reached plateau height and then it gradually commenced to fall away. On the reasoning developed above this suggests that there was first an increase of E and then a gradual lowering of it in the subliminally excited neurones. Associated with this there is in time a reduction to below threshold of the E in those neurones supraliminally excited as is shown by the tension gradually falling. This process which we believe to be allied to fatigue needs much more investigation before its exact nature is ascertained. An alternative explanation would be that this fatigue process is a condition allied to adaptation, whereby the neurone becomes less responsive to the exciting influence of the E substance.

Our results have supported the distinction made (17), (18), (19) between the extensor type of reflex and the flexor type. Though we have frequently found crossed extensor reflexes approaching the "d'emblée" type, and have never seen the slow recruiting rise (in a deafferented preparation) unaccompanied by inhibition, a fundamental difference between the crossed extensor and the flexor reflexes lies in the former's marked power of summation and after-discharge as shown by concurrent and sustained

facilitation respectively. In this it is more closely allied to the fundamental properties displayed by the higher parts of the nervous system, than is the ipsilateral spinal flexor reflex which is simpler and which shows certain resemblances in behaviour to the transmission of impulses from motor nerve to muscle (17), (18). One is struck by the many similarities in behaviour between the scratch reflex⁽²²⁾ and the crossed extensor reflex. Thus temporal and spatial summation and after-discharge are in both striking features. One has yet to discover whether their difference from the flexor type of reflex is due merely to their more complex reflex path, or if there is some special summational property of either the internuncial or motor neurone.

V. SUMMARY.

1. In a preliminary account of crossed extensor reflexes in the de-afferented preparation the various modifications of latent period, recruitment, and after-discharge are described. Recruitment is often found to be a very rapid process.

2. Crossed extensor reflexes of various fractions of quadriceps are recorded simultaneously, and it is found that, while vastus lateralis and vastus medialis are similar in behaviour, rectus femoris presents many striking differences when compared with a simultaneously recorded vastus medialis. The peculiar behaviour of rectus is possibly associated with its specialised function as a double joint muscle.

3. In contrast with flexor reflexes facilitation is a very prominent feature in the interaction of crossed extensor reflexes.

Two sub-groups are described:

(a) When the effect is exerted by one reflex on another concurrently excited (concurrent facilitation).

(b) When it appears as the after-effect of one reflex on another (sustained facilitation).

4. The facilitating power of one weak reflex on another is not maximal until its recruitment is almost complete, and soon after this it again diminishes, apparently owing to some fatigue process. There is, therefore, an optimal point of facilitation.

5. An invariable shortening of latent period accompanies facilitation.

6. In many respects occlusion, as exhibited in the interaction of two crossed extensor reflexes, is found to have features in common with a similar phenomenon in flexor reflexes.

7. The presence of inhibition in some reflexes and the possible influence of its presence on interaction is considered.

8. The nature of facilitation is discussed and, from the data obtained, one is compelled to postulate the accumulation of some excitatory substance in the neurone. The Sherrington conception is thus supported.

9. Sustained facilitation is shown to be an index of subliminal after-discharge.

10. The evidence obtained also supports the distinction which Liddell and Sherrington have made between the extensor and flexor types of reflex.

We wish to express our thanks to Sir Charles Sherrington and to Dr Denny-Brown for valuable advice, and to the Christopher Welch Trustees for defraying the cost of the photographic material.

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