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EXCITATORY AND INHIBITORY SKIN AREAS FOR FLEXOR AND EXTENSOR MOTONEURONES

By

K.-E. HAGBARTH

#94

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Ivar Hæggströms Boktryckeri A. B.
Stockholm 1952

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PREFACE

The experiments presented in this thesis were carried out at the Nobel Institute for Neurophysiology in Stockholm. It is a pleasure to record my gratitude to the Director of this Laboratory, Professor **Ragnar Granit**, for valuable advice and encouragement and for his kindness in placing at my disposal instruments and facilities in his laboratory.

I am also greatly indebted to Dr. B. **Frankenhæuser** for valuable criticism of my work and for all the interest he has shown in it.

The investigation has been supported by grants from the Swedish Medical Research Council and the Rockefeller Foundation to the Nobel Institute for Neurophysiology as well as by personal grants to the author from "August och Thérèse Hazelius' fond" and "Lindahls fond" of the Royal Swedish Academy of Sciences.

Stockholm, February 1952.

KARL-ERIK HAGBARTH

INTRODUCTION

The theme of this work arose as a consequence of previous experiments carried out in this laboratory. Attention had been drawn to the possibility of exciting ipsilateral extensor motoneurones by stimulating cutaneous nerves of the limb (HAGBARTH and NAESS 1950 a). Considering that cutaneous afferents have generally been held to constitute a link in the flexor reflex our results seemed somewhat remarkable. It was felt that this subject deserved an experimental survey and so the present study was begun in order to expand the analysis of spinal reflex responses elicitable from cutaneous afferents of the limb and the appropriate receptors in the skin.

It has long been known that flexion of the limb can be evoked by stimulating the skin of the limb or its afferent nerves. This flexor reflex of the limb was systematically studied by SHERRINGTON in 1910. He stated that whichever cutaneous nerve trunk was stimulated in the limb, the reflex in the limb muscles was essentially the same; the general effect throughout was excitation of the motoneurones of flexors and inhibition of the motoneurones of extensors. The receptive field of the flexor reflex was found to include "the skin of the whole limb as far up as the groin in front, the perineum medially and the ischial region behind" (p. 32).

These original findings have been followed by innumerable investigations concerning the nature and properties of the flexor reflex. It was recognised quite early, however, that the general rule of "ipsilateral flexion" was broken by some exceptions. Thus the "extensor thrust", described by SHERRINGTON in 1903, represents one exception to the rule. By pressing the skin underneath the toe-pads of the hind-foot in dogs it proved possible to evoke an extension of the limb (cf. "the positive supporting reaction": MAGNUS 1926; SCHOEN 1926 and PRITCHARD 1926). Since a nociceptive stimulus to the same plantar region caused the typical flexor reflex it was concluded that different kinds of end-organs within the same cutaneous region may possess spinal reflex connexions of opposite character.

Ipsilateral extension has also been obtained upon stimulation of peripheral nerve trunks. Thus Sherrington and Sowton (1911) found that weak galvanic stimuli tended to produce an ipsilateral extension which was more difficult to excite with the common type of faradic stimulus. In a similar investigation Graham Brown and Sherrington (1912) concluded that an ipsilateral cutaneous nerve sometimes yields reflex contraction of extensor muscles.

Of great interest in this connexion are some papers by Graham Brown (1911; 1912). In these experiments reflex movement of the muscles acting upon the ankle joint was obtained by electrical stimulation of a cutaneous nerve of the limb. There was great variability in the response and it was concluded that an ipsilateral stimulus does not merely activate the flexor and inhibit the extensor mechanisms but that it also inhibits the flexors and activates the extensors, although the latter effects may be masked by the dominant flexor reflex (cf. Ranson and Hinsey 1930).

These observations agree with those reported by Denny-Brown (1938) who called the hidden excitatory extensor reflex the "residual ipsilateral extension". Ipsilateral extension has also been seen with higher frequency stimulation of afferent nerves (Bernhard and Skoglund 1942).

In most of the papers mentioned only the reflexes of the hind limbs have been examined. In 1928 Denny-Brown and Liddell presented evidence to the effect that in the fore-limbs also there is departure from the rule that electrical stimulation of a limb nerve causes withdrawal of that limb. Thus activation of an ipsilateral extensor muscle could be set up by stimulating the median nerve or the skin of the radial border of the forearm. The authors suggested that the extensor reflexes elicitable from ipsilateral afferent nerve trunks, the extensor thrust and the positive supporting reaction, are phases of activity of the same reflex mechanism under different conditions. It must, however, be emphasized that the afferent path of the extensor thrust is restricted to the plantar nerves (Sherrington 1907) whereas the afferent

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sources of extensor excitatory effects following nerve trunk stimulation are more widely distributed.

From the experiments of Renshaw (1940) and Lloyd (1943 a, b and c, 1946 a and b) it became evident that in order to study reflex effects it is not necessary to preserve intact efferent supply. Indeed, ~~an intact~~ efferent supply is a complicating factor because of the antidromic effects set up by stimulation of mixed nerve trunks. To avoid this complication the size of the monosynaptic response (Eccles and Pritchard 1937), elicited from a peripheral muscle nerve and recorded from a severed ventral root, may by used as a test of motoneurone excitability. By using this method of recording Lloyd studied the reflex functions of different afferent fibre groups in the hind limb. He stated that the response to a single shock to an ipsilateral skin nerve is indirect facilitation of the flexor motoneurones and a likewise indirect reciprocal inhibition of the extensor motoneurones. This is Sherrington's flexor reflex with its reciprocal extensor inhibition.

In 1947 it was pointed out by Bernhard that not only an inhibition, but also a later facilitation of extensor motoneurones, could be evoked by a single shock of a skin nerve. This finding was confirmed by Hagbarth and Naess (1950 a) who also found that during prolonged tetanic stimulation of a cutaneous nerve a continuous state of extensor facilitation could be maintained.

Thus to sum up: by myography as well as by monosynaptic testing exceptions have been found to the rule that ipsilateral skin reflexes of the limb consist in flexor excitation and extensor inhibition. Very little seems to be known about these "exceptions" the interpretation of which will now be elucidated.

It will be shown that the nature of the response is fundamentally determined by that particular skin area of the limb to which stimulation has been applied. For both flexor and extensor muscles, specific excitatory and inhibitory skin areas have been found. Each of the extensor muscles studied was inhibited from most parts of the limb but excited from a skin area mainly localized over the muscle itself. Each of the flexor muscles was excited from most parts of the limb but inhibited from a skin area mainly localized over the antagonistic extensor muscle.

METHODS

Preparations. The experiments were performed on cats. All the animals were decerebrated during ether anaesthesia after ligation of the carotid arteries. In most instances the spinal cord was transected at about Th 8—10. Two hours were allowed for removal of the anaesthesia before the experiment was begun.

In most experiments the spinal cord was exposed in the lumbar region. The left ventral roots L5—S2 were cut and the central stumps dissected free to be used for the recording of monosynaptic test reflexes. In the left hind limb one or several muscle nerves were severed peripherally and isolated for the stimulating test electrodes. Sometimes ipsilateral cutaneous nerves were similarly prepared for the conditioning stimulus, but in other experiments they were left intact so that excitation could be set up by adequate means from the end-organs of the skin (Fig. 1). As a rule the contralateral limb was denervated.

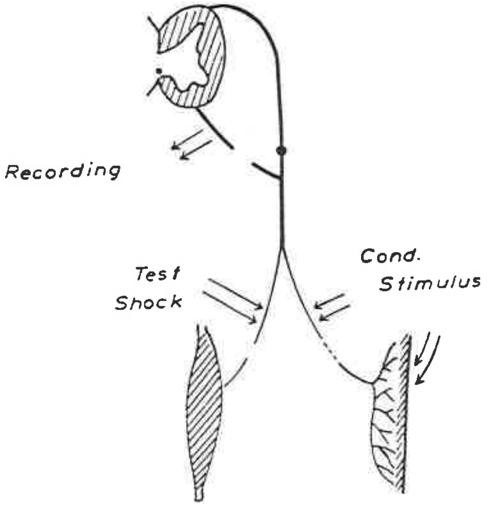

Fig. 1. Diagram illustrating experimental arrangement when the monosynaptic method is used.

In another series of animals the efferent supply was kept intact. The muscle to be investigated was usually isolated from the rest of the musculature but sometimes only the tendon of the muscle was dissected free for attachment to the spring myograph.

Fixation. During operation and recording the animals were placed on a heated table. During recording they were held by clamps which gripped spinal processes. When myographic recording was used the cats were also fixed with drills through the condyle of the femur and the lower part of the tibia. The exposed tissues, the nerves as well as the spinal cord, were immersed in liquid paraffin.

Stimulation. Single shock stimuli could be released at regular intervals by synchronization with the sweep. Two stimulators with rectangular pulses were triggered by a delay circuit. The stimulating electrodes were small silver hooks with an interpolar distance of about 5 mm.

In some experiments thermal stimulation of cutaneous afferents was employed. The nerve rested in a small metal container (thermode), the temperature of which could be regulated by circulating water (cf. C. v. Euler 1947). The temperature of the container was measured by means of a thermocouple connected to a Cambridge spot galvanometer. The accuracy of the temperature records was about ± 1.0°.

Recording. The nerve impulses were led off by electrodes similar to the stimulating ones. For recording of muscle action potentials the electrodes consisted of silver pins or of small electrodes in the shape of steel needles, isolated down to the tip. A condensor-coupled amplifier and cathode-ray tubes were used for recording. Muscle tension was recorded with a myograph consisting of a strain gage instrument (Karlén och Ljungström 1946) connected to one of the cathode-ray tubes. Photographs were taken on bromide paper.

The muscles used in the present investigation have been chosen because of the relative simplicity of their mode of action.

In many experiments the extensor muscles of the ankle have been used. Anatomically there are four muscles to be recognised:

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the medial and lateral parts of gastrocnemius, plantaris and soleus. In this work no distinction has been made between them. They have merely been regarded as components of a muscle bundle with a unitary action.

The anterior tibial muscle has been chosen because of its uncomplicated function as a flexor muscle of the ankle. It is the main antagonist to the extensor calf muscles.

Among the muscles acting upon the knee the quadriceps muscle has been chosen to represent the extensor group. Its rectus component is also a flexor of the hip and has therefore always been removed. As an antagonist flexor of the knee the semitendinosus muscle has been used.

Finally some muscles acting upon the toes have been studied. The antagonistic muscles investigated are the extensor brevis digitorum and the flexor brevis digitorum, the former acting in dorsiflexion the latter in plantarflexion of the toes.

RESULTS

REFLEX EFFECTS OF SKIN AFFERENTS FROM DIFFERENT PARTS OF THE LIMB

Single shock stimulation of cutaneous nerves.

In these investigations a single electrical shock was applied to an ipsilateral cutaneous nerve. The ensuing excitability changes in the motoneurones of different muscles were evaluated by recording monosynaptic test reflexes from a ventral root.

In the first experiments the test shock was applied to the nerve of the ankle extensors. Fig. 2 presents an example of excitability changes in the extensor nucleus following a shock to the sural nerve. The initial effect is a depression of the excitability but subsequently the curve turns into facilitation (cf. BERNHARD 1947). In the majority of experiments these events were quite

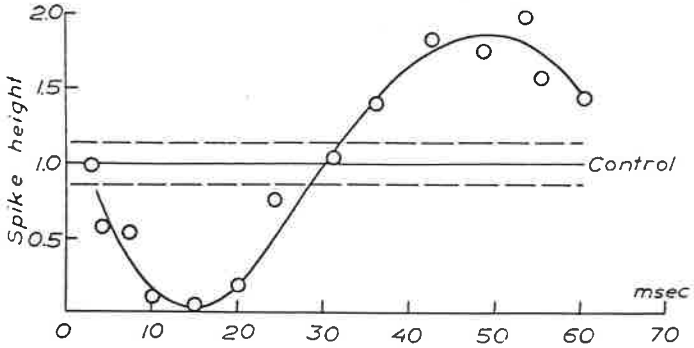

Fig. 2. Spinal cat. Excitability changes in the motoneurones of the ankle extensors following a conditioning shock to the sural nerve. The control lines show the average and the extreme values of ten independent readings and each circle represents the mean value of two readings (as in all succeeding curves).

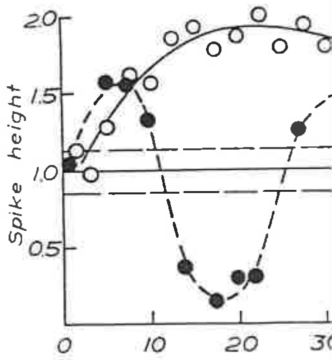

Fig. 3. Decerebrated cat. Excitabilit
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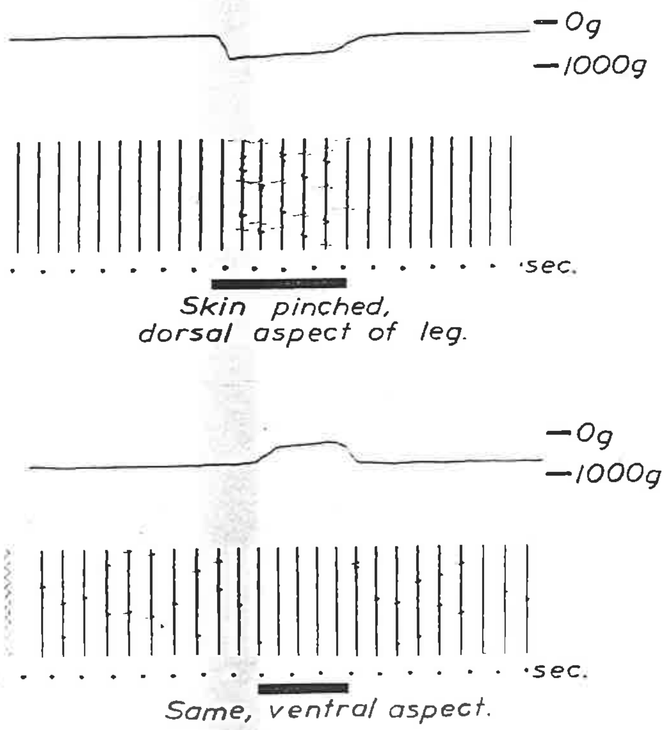

Fig. 12. Decerebrated cat. Records showing the tension and the electrical activity of the extensor muscles of the ankle. The muscular activity is influenced in opposite ways from different skin areas of the limb. Time in 10 msec. (on the left).

myographic method, were in accordance with those found by the monosynaptic method of testing. The excitatory skin area as a rule was localized over the heel and the calf. From the toe-pads, the dorsal aspect of the thigh and the whole ventral surface of the limb the usual effect was inhibition (cf. Fig. 11).

At times conditions did not at once return to normal after stimulating the skin. Different kinds of secondary effects were noted. An excitatory or an inhibitory effect may remain and slowly decline during some seconds after pinching. But it also happens that the pinch is rapidly followed by an effect opposite to the immediate one. These inconstant phenomena have been recorded both by myography and monosynaptic testing.

In the experiments described the results have been obtained by pinching the skin of the limb. This mode of stimulation is adequate for many different kinds of cutaneous nerve endings. The end-organs of touch pressure and pain are indiscriminately activated and it is difficult to know what part each of these receptor groups plays in the reflex reactions described.

As a rule the intensity of the reflex response was increased when the pinch was made harder. It often happened that from certain points of the skin no effects could be evoked by the mechanical stimulus unless it was of an obviously noxious kind. The impression was obtained that, though the tactile component by itself sometimes was sufficient to evoke the reflex responses described, a maximal effect could never be obtained until the noxious component was involved. To get further information concerning the end-organs involved different modes of stimulation were used.

Pressure. By the finger-tip or a piece of cotton wool moderate pressure was applied to the shaved skin surface. The stimulus was just strong enough to cause a small visible deformation of the skin. When this stimulus was used to map the limb by means of the effects as read off in the motoneurones of the ankle extensors, it turned out that from many areas of the skin no effects at all could be evoked. In most experiments, however, certain regions were found from which the stimulus had an obvious influence upon the amplitude of the monosynaptic test reflexes.

Sometimes a weak inhibitory effect was obtained from the skin over the knee, sometimes a similar effect could be evoked only from some other region on the ventral side of the limb. In no experiment was it possible to demonstrate any obvious effects from the upper or plantar aspect of the foot, from the dorsal aspect of the thigh or from the proximal part of the calf. When applied to the lower part of the calf or the region over the heel, however, the moderate pressure sometimes caused excitability changes of the extensor motoneurones. The effect obtained from this skin area was always a facilitatory one.

Touch. In some experiments the hairy coat was left intact and stimulation was obtained by touching the hairs with cotton wool.

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In both decerebrated and spinal cats this mode of stimulation usually failed to elicit any muscular responses. It was found, however, that if a normal cat, intact and quite awake, be lifted up and stimulated in this way over the heel, then it sometimes happens that a marked extension at the ankle joint supervenes.

Cold, warmth, heat. A thermode consisting of a small metal container (10 mm × 5 mm) was applied to the skin surface and the temperature was regulated by means of circulating water. The thermode was applied to different areas of the limb and the effect of cold and warmth was studied in the motoneurones of the ankle extensors. Moderate changes of the temperature (25—45°) never elicited any visible reflex responses, but when the temperature rose to give injurious heat (above 50°), then there was often an influence upon the amplitude of the test reflexes. When an obvious effect was obtained from the ventral side of the leg or from the foot, it was an inhibitory one, but from the calf and the region over the heel excitatory effects were evoked.

Taken together the results show that though noxious pinch is the most efficient mode of stimulation for mapping excitatory and inhibitory skin areas of a certain muscle, similar results can be obtained also by other kinds of stimuli. By varying the modes of stimulation no qualitative changes of the results were obtained. When an effect upon the motoneurones of the ankle extensors was evoked from the skin over the calf and the heel, it was always an excitatory one, independent of what kind of stimulation had been employed. Similarly when an effect was evoked from other parts of the limb it was always an inhibitory one. As to the receptor organs responsible for the effects it can be concluded that nociceptive nerve endings as well as tactile end-organs are concerned, while those responding to temperature changes are not of the same importance.

In several experiments records were taken of excitability changes in the motoneurones of tibialis anterior, the flexor muscle of the ankle (Fig. 13 A). Monosynaptic test reflexes were elicited from the nerve of this muscle and recorded from the ventral root L7. When pinching the skin of the calf a marked inhibition was

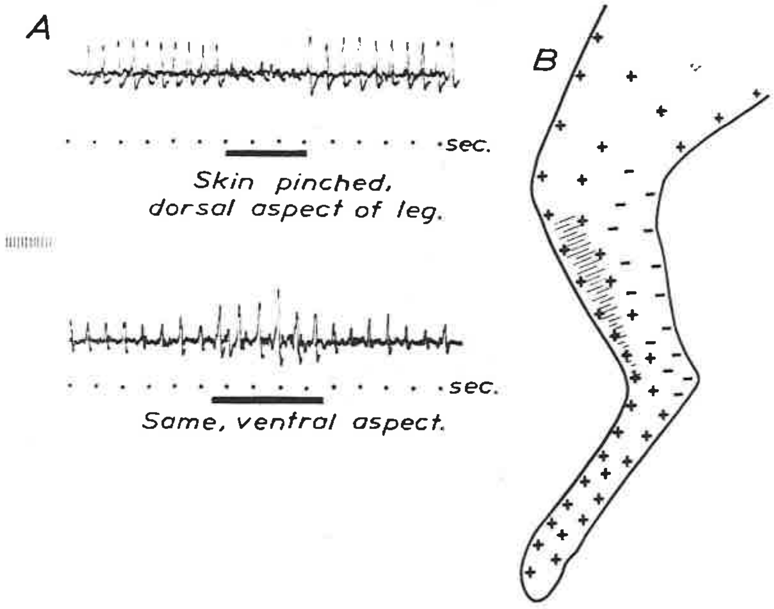

Fig. 13. *A*. Spinal cat. Records from the ventral root L7. Monosynaptic test volleys obtained from the nerve of tibialis anterior. There is an inhibitory effect from the skin over the calf, but from the ventral aspect of the leg a facilitatory effect is evoked. Time in msec. (on the left). *B*. Spinal cat. Diagram showing the extent of inhibitory and excitatory skin areas for tibialis anterior.

evoked (above) but, when the stimulus was applied to the ventral aspect of the leg, it gave an excitatory effect (below).

As a rule inhibition could be elicited from a skin area on the dorsal side of the limb extending from the popliteal space to just below the heel. From the rest of the limb excitation was the usual effect (Fig. 13 B).

The inhibitory skin area for the flexor muscle of the ankle must be compared with the excitatory region found for the antagonist extensor muscles (see Fig. 11). If the innervation is strictly reciprocal these two skin areas should be identical. They actually look quite similar even if the boundaries are too diffuse to permit precise comparison.

In order to prove that the flexor inhibition really was accompanied by a relaxation of the muscle the myographic method was

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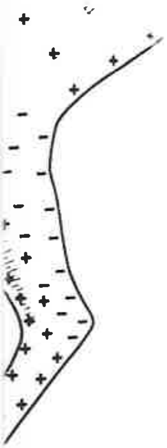

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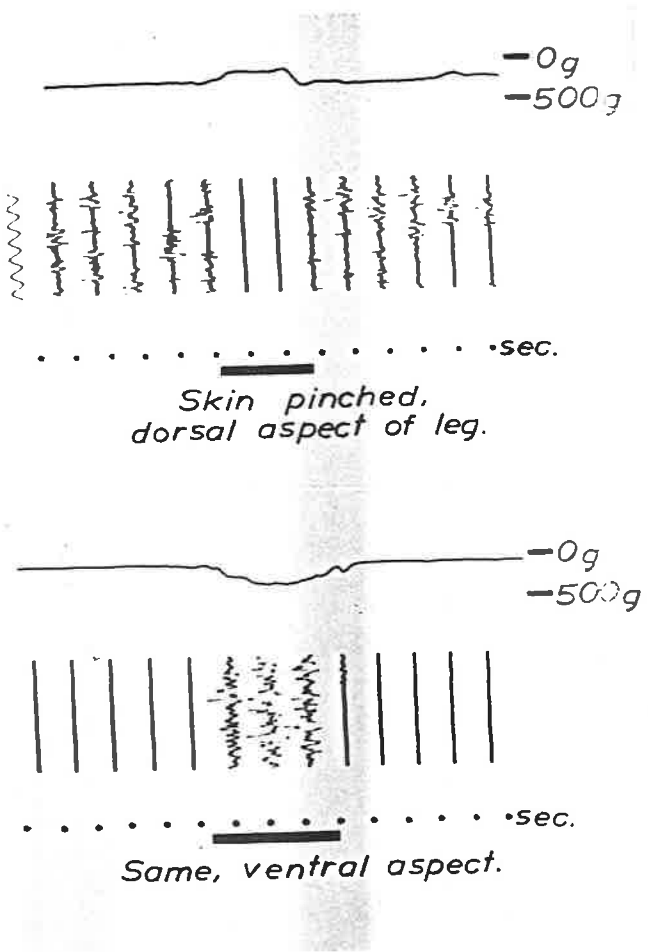


Fig. 14. Spinal cat. Records showing how the tension and the electrical activity of tibialis anterior is influenced from different skin areas of the limb. Time in 10 msec. (on the left).

used. The tendon of tibialis anterior was attached to the myograph and impulses were recorded by electrodes inserted into the fleshy portion of this muscle. Pinching the skin of the calf gave relaxation of the muscle (Fig. 14 above); contraction appeared when the stimulus was applied to the ventral aspect of the leg (below).

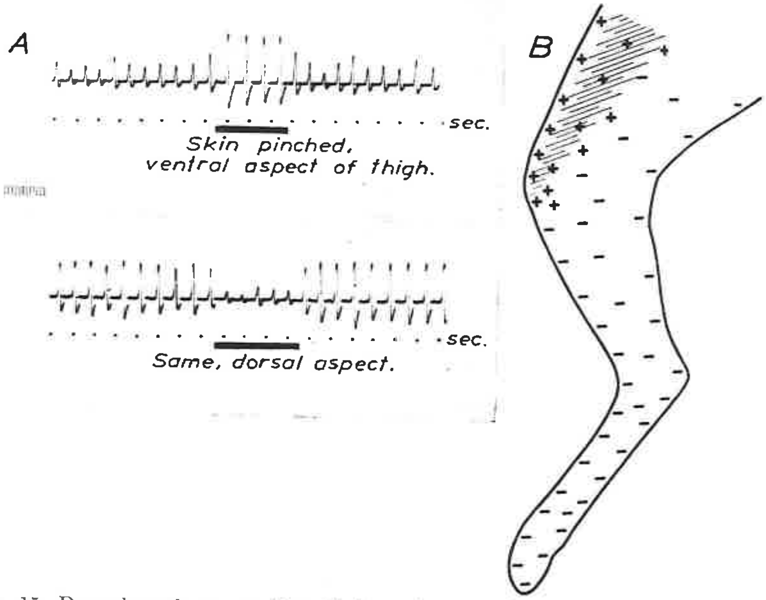
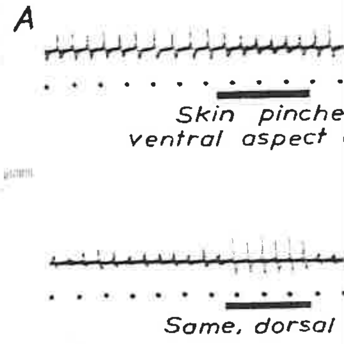


Fig. 15. Decerebrated cat. *A*. Records from the ventral root L6. Monosynaptic test volleys obtained from the nerve of the knee extensors. Facilitation is evoked from the skin on the ventral aspect of the thigh and inhibition from the dorsal aspect. Time in msec. (on the left). *B*. Diagram showing the extent of inhibitory and excitatory skin areas for the extensor muscles of the knee.

Sometimes monosynaptic test reflexes were elicited from the nerve of the knee extensors and recorded from the ventral root L6. The cutaneous innervation was left intact and by pinching the skin, mapping of the limb could be performed by means of the effects read off in the extensor nucleus. From the main part of the limb an inhibition was obtained, but from a skin area on the ventral side of the limb, extending from the proximal part of the thigh to just below the patella, marked facilitation could be evoked. The zone of maximum excitation was as a rule at the knee (Fig. 15).

Thus it is evident that different extensor muscles of the limb do not behave alike in response to ipsilateral skin stimuli. Both the extensor muscles studied have been inhibited from the principal part of the limb, but each of them had a circumscribed skin area from which excitatory effects arose. Furthermore, these



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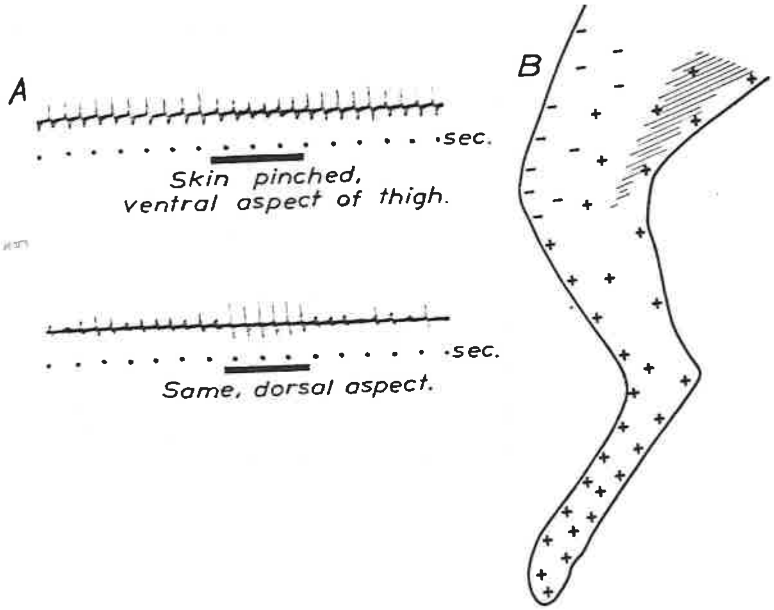


Fig. 16. Spinal cat. *A*. Monosynaptic test reflexes elicited from the nerve of the semitendinosus muscle and recorded from the ventral root SI. The reflexes are inhibited from the skin on the ventral aspect of the thigh and facilitated from the skin on the dorsal aspect. Time in msec. (on the left). *B*. Diagram showing the extent of inhibitory and excitatory skin areas for the semitendinosus.

excitatory zones were not identical for the two muscles. They were mainly localized over the individual extensor muscles concerned.

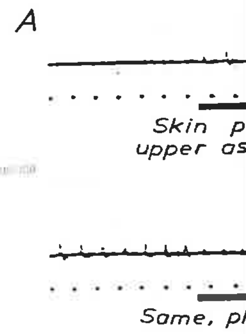
An antagonist to the extensor muscles of the knee is the semitendinosus. From the nerve of this muscle it has sometimes been difficult to elicit any monosynaptic reflexes. When present, they have usually been small and therefore inhibitory effects not easy to demonstrate. In Fig. 16, however, an experiment is presented in which both excitatory and inhibitory effects could be elicited from the skin. From the plantar and upper side of the foot the excitatory effects were quite strong. From the calf and the dorsal aspect of the thigh it was difficult to evoke any marked effect but, when an effect was seen, it was an excitatory one. From the ventral aspect of the thigh, however, inhibition could be obtained and the distribution of the inhibitory region seemed to coincide fairly well with the excitatory skin area for the extensor muscles of the knee (see Fig. 15).

The extensor brevis digitorum is a small thin muscle on the upper side of the foot and it acts in dorsiflexion of the toes. It is innervated by a branch of the deep peroneal nerve. It was difficult to isolate this small muscle nerve and apply electrodes to it. Therefore the test shock was applied to a somewhat larger branch of the deep peroneal nerve which, besides innervating the extensor brevis digitorum, also takes part in the innervation of the skin.

In many spinal animals it proved impossible to elicit any monosynaptic reflexes from this nerve. But in decerebrated cats small monosynaptic responses could sometimes be recorded from the ventral root L7. It turned out that facilitation of the test responses to pinching of the skin could be obtained from an area on the upper side of the foot, extending from the toes to just above the ankle (see Fig. 17). Because of the weakness of the monosynaptic reflexes inhibition was more difficult to demonstrate. Two different methods were employed in order to increase the control level of the test reflexes. Sometimes a spring-holder was attached to the skin on the upper side of the foot. Thus a constant stimulus with long duration was obtained. In this way an increase of the reflexes could often be maintained for about 10—20 sec. and thus a background of excitation obtained for inhibitory influences to set themselves off against.

In other cases the post-tetanic potentiation (LARRABEE and BRONK 1947) was made use of (LLOYD 1949; ECCLES and RALL 1951). A tetanic stimulation (100—200/sec.) was applied to the nerve and during the ensuing potentiation of the monosynaptic responses inhibitory influences from the skin could be studied.

The zone of maximum inhibition of the extensor brevis digitorum turned out to be the plantar surface of the foot. Especially from the proximal toe-pad there was marked depression. From calf and thigh the effects were much weaker and by no means constant. Quite often no effects whatever could be evoked from these large skin areas of the limb. In a few experiments, however.



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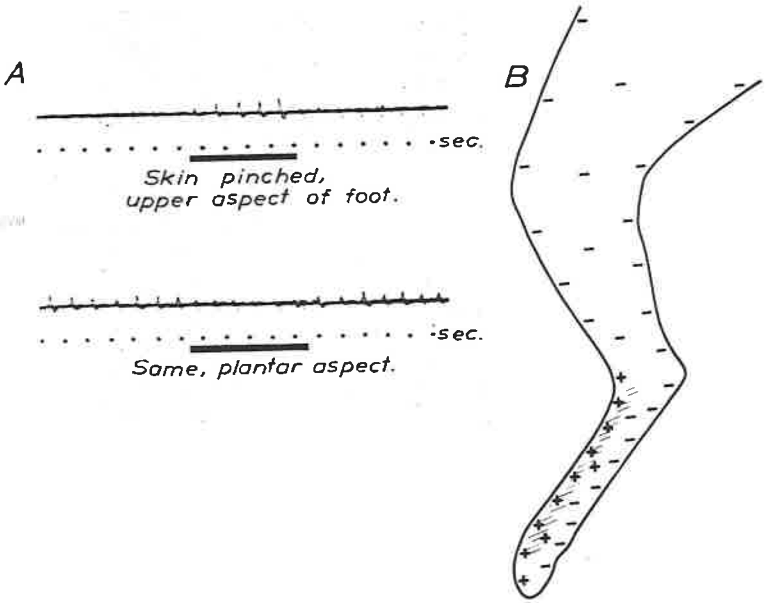

Fig. 17. Decerebrated cat. *A*. Monosynaptic test reflexes elicited from the nerve of the extensor brevis digitorum and recorded from the ventral root L7. The reflexes are facilitated from the skin on the upper aspect of the foot and inhibited from the skin on the plantar aspect. Time in msec. (on the left). *B*. Diagram showing the extent of inhibitory and excitatory skin areas for the extensor brevis digitorum.

it was quite obvious that inhibitory influences could be initiated both from the ventral and dorsal aspects of leg and thigh (Fig. 17).

Finally the flexor brevis digitorum was investigated. This muscle, localized on the plantar side of the foot, is innervated from a branch of the medial plantar nerve. In most experiments this nerve has been stimulated by the test electrodes. In some decerebrated animals no monosynaptic reflexes were obtained but in an experiment in which a spinal cat was used, monosynaptic responses could be read off in the ventral root S2 (Fig. 18). The test reflexes were facilitated from most skin points of the limb and most easily from the plantar surface of the foot. From the upper aspect of the foot, however, inhibition was obtained. The in-

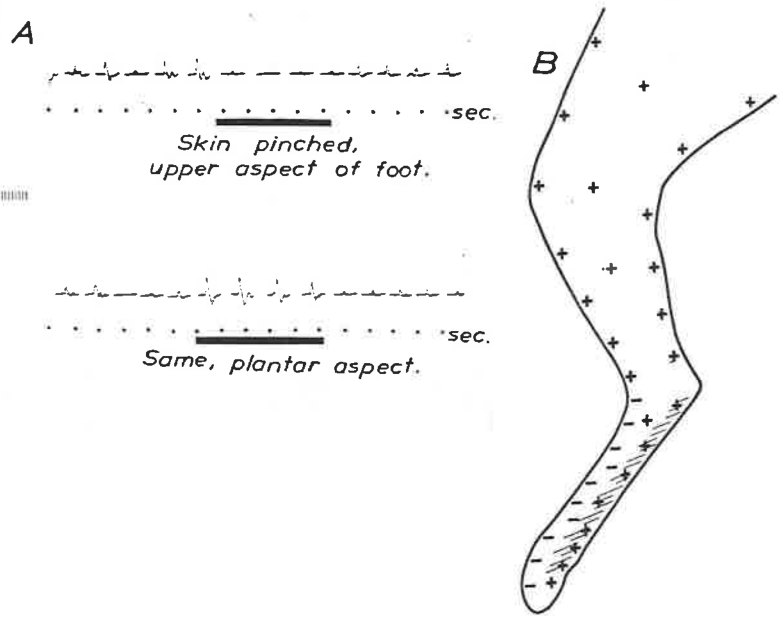

Fig. 18. Spinal cat. *A*. Monosynaptic test reflexes elicited from the medial plantar nerve and recorded from the ventral root S2. The reflexes are inhibited from the skin on the upper aspect of the foot and facilitated from the skin on the plantar aspect. Time in msec. (on the left). *B*. Diagram showing the extent of inhibitory and excitatory skin areas for the flexor brevis digitorum.

hibitory skin area showed an obvious resemblance to the excitatory area found for the antagonistic muscle on the upper side of the foot (cf. Fig. 17).

DISCUSSION

When studying the flexor reflex, **Sherrington** (1910) found that the localization of the stimulus influences the character of the movement. It was stated that the reflex elicitable from a certain afferent nerve of the limb "is not of necessity wholly like that produced from some among the other afferents of the limb" (p. 38). Similarly it was shown that different skin points of the limb were not quite equivalent with respect to their reflex effects:

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"there comes to be some accentuation of movement at this joint or that according as the skin-point stimulated lies in this limb-region or that" (p. 39). These phenomena, however, were described as various forms of the general flexor reflex. The contraction should in all cases be restricted to the flexor group of muscles.

It has been confirmed by the present investigation that the localization of the ipsilateral skin stimulus is an important factor in determining the character of the reflex response; this, however, not only with regard to the extent of the movement but also with regard to its direction. It has been shown that the contraction is not always limited to the flexor group of muscles. From certain skin-points of the limb extensor excitation and flexor inhibition can be evoked.

The experiments have demonstrated the importance of physiological conditioning. The results obtained by stimulation of cutaneous nerves cannot be fully understood unless compared with those obtained by adequate stimulation of skin end-organs. From the experiments with electrical and thermal stimulation of cutaneous nerves it was concluded that the skin nerve trunks contain sensory components, functionally connected to the musculature in opposite ways. The results did not support the assumption that fibre size is the basis of this physiological subdivision. Similar effects were obtained from large and small cutaneous afferents. The only way in which some kind of afferent selectivity could be obtained was by stimulating different skin nerves.

The findings with thermal and electrical stimulation were confirmed and appeared in new light when it was demonstrated that for both flexor and extensor muscles specific excitatory and inhibitory skin areas could be mapped out. In the same way as the reflex effects were similar for large and small skin fibres so also were they qualitatively similar for different kinds of adequate skin stimuli. It is well known that different modalities of cutaneous sensation cannot be strictly referred to definite fibre sizes (Gasser 1943). Touch alone in the cat elicits a variety of spikes of different conduction rates (Zotterman 1939). On the other hand, it is evident that nociceptive impulses are conducted in relatively thin fibres while tactile impulses are partly, at least, conveyed in large ones (ADRIAN 1931, HEINBECKER, BISHOP and O'LEARY 1933; CLARK, HUGHES and GASSER 1935; ZOTTERMAN 1939).

In this connexion it is necessary to review some previous observations showing that under certain conditions different reflex responses can be evoked from different kinds of end-organs belonging to one and the same cutaneous region. The extensor thrust as described by SHERRINGTON is of special interest. He stated (1903) that if in a spinal dog the skin underneath and between the toe-pads and cushion of the hind foot was pressed or stretched a sudden forcible extension of the limb was evoked. But when a harmful stimulus such as a prick was applied to the same pad region, then flexion of the limb occurred.

In the present investigation the extensor thrust reflex has not been met with. A noxious pinch of the plantar region caused inhibition of the motoneurones of the ankle extensors but a moderate pressure applied to the same skin area had no visible influence upon the excitability of the extensor nucleus (p. 28). In the experiments described, however, the tactile stimulus was just strong enough to cause a slight deformation of the skin surface and it is possible that this is not an adequate mode of stimulation for the extensor thrust. In the present investigation it was never noted that different kinds of stimuli applied to one and the same cutaneous skin area yield opposite reflex responses in the musculature. It must be pointed out, however, that the different kinds of stimuli used do not exhaust all possibilities. Thus on the basis of the results obtained it cannot be definitely excluded that under certain conditions not only the localization of the stimulus but also the mode of stimulation might influence the nature of the reflex response.

In anatomical nomenclature the muscles acting in dorsiflexion of the toes are named extensors and those acting in plantar flexion are named flexors. From the physiological point of view, however, there is evidence that the dorsiflexors are functionally allied to the flexor group of muscles (SHERRINGTON 1910; WALSHE 1915).

Now, it must be emphasized that the extensor longus digitorum besides acting in dorsiflexion of the toes also causes flexion at the ankle. A muscle with such a complicated action is not adapted to a strict functional classification. It might be flexor at one joint

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but extensor at another. As to the extensor brevis digitorum, however, the matter is different. It only acts in dorsiflexion of the toes and a classification of this muscle as a flexor implies that dorsiflexion of the toes must be regarded as a flexion movement while plantar flexion should be regarded as an extension.

It is evident that a functional classification always depends upon which criteria have been used. If in response to an afferent stimulus flexion at hip, knee and ankle is accompanied by a contraction of the extensor brevis digitorum it certainly cannot be concluded that this muscle is functionally allied to the flexor group of muscles. It all depends upon the stimulus itself. It has been shown above that, from certain skin areas of the limb, extensor-excitation and flexor-inhibition can be evoked. A certain muscle cannot therefore be classified as a flexor, merely because of the fact that it contracts in response to an ipsilateral nociceptive stimulus of the skin. It may, in fact, relax to another similarly nociceptive stimulus applied to the skin in the neighbourhood.

The results of the present investigation have shown a resemblance between the extensor brevis digitorum and the extensor muscles of knee and ankle. These muscles were all inhibited from most points of the limb but excited from a skin area mainly localized over the muscle itself. On the other hand, the flexor brevis digitorum functionally behaved as the flexor muscles of knee and ankle. It was facilitated from most points of the limb but inhibited from a skin area mainly localized over the antagonistic extensor muscle.

In these respects it is thus evident that the extensor brevis digitorum is functionally allied to the extensor muscles and that the flexor brevis digitorum is functionally allied to the flexors. It should also be noted that monosynaptic reflexes from the nerve of the extensor brevis digitorum were more easily evoked in decerebrated than in spinal animals and that the reverse held true when the flexor brevis digitorum was concerned. Since it is well known that monosynaptic reflexes from extensor muscles are favoured by the extensor tonus of a decerebrated animal, these observations fall well in line with the functional classification described.

The fact that different limb muscles can apparently be excited and/or inhibited by stimulation of specific skin areas indicates a rather new concept which suggests certain conclusions. When studying the influences from the skin upon the musculature of the limb each muscle must be studied separately. As a rule, when the myographic method is used, this condition is fulfilled but the monosynaptic method sometimes involves risks. In many previous investigations monosynaptic test responses have been elicited from the deep peroneal nerve. In such experiments the muscles innervated by that nerve have been treated as a functional unit. But among these muscles there are both the tibialis anterior and the extensor brevis digitorum which in the present investigation have been shown to behave quite differently in response to ipsilateral stimulation of the skin. In previous work monosynaptic reflexes, elicited from the deep peroneal nerve, have sometimes been conditioned by electrical stimulation of a cutaneous nerve trunk. (Lloyd 1943 b; Bernhard 1947; Hagbarth and Naess 1950 a). Undoubtedly the interpretation of such experiments is difficult. Not only the conditioning influx from the cutaneous nerve but also the test volley itself might be of a compound character. In view of these circumstances it is not surprising that stimulation of cutaneous nerves does not necessarily condition the deep peroneal monosynaptic response opposite to the way in which it affects the gastrocnemius monosynaptic volley (cf. Hagbarth and Naess 1950 a).

It has been shown that the excitatory skin areas of extensors are mainly localized over the extensor muscles concerned. This fact seems to have some significance. But before any further conclusions are drawn concerning the fundamental organization behind the phenomena described, another problem must be dealt with. Has the dorsal root distribution of skin afferents anything to do with the reflex effects elicitable from the skin? Is there any obvious correspondence between the dermatomes of the limb and the distribution of excitatory and inhibitory skin areas for a certain muscle? This question will be elucidated in the following chapter.

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THE DORSAL ROOT DISTRIBUTION OF SKIN AFFERENTS WITH DIFFERENT REFLEX EFFECTS

The extensor muscles of the ankle are segmentally innervated from S1 and in some cases also from L7. It has been shown that they are excited from a skin area on the dorsal side of the limb extending from just above the knee to just below the heel. From other parts of the limb they are inhibited.

The distribution of the dermatomes in the cat has been thoroughly investigated by KLESSENS (1914), and from his description it appears that the dermatome of S1 is chiefly localized on the dorsal side of the limb and extending from the dorsal aspect of the thigh to just below the heel. Thus it is evident that this dermatome resembles the excitatory skin area found for the ankle extensors.

The following experiments supply further evidences that the nerve supply of the ankle extensors and the nerve supply of their excitatory skin area lie segmentally near together.

a. In some experiments the excitatory skin area for the ankle extensors was mapped before and after severance of the dorsal roots L5, L6, L7 and S2. The only root left was S1 in which the monosynaptic test volley passed. In all cases excitatory effects could be obtained after severance of these roots but usually not from as large a skin area as before. As a rule the excitatory effect from the heel was unchanged (sometimes it even appeared to be increased) but from the skin more proximally on the calf the excitatory effect had often disappeared. That is to say, the cutting made the excitatory area somewhat smaller but from the excitatory region that still remained the effect had, if anything, increased.

In one single experiment it was quite obvious that after the section a skin area, just below the popliteal space, was changed from an excitatory region into an inhibitory one. When all roots were intact it was quite easy to obtain excitatory effects from the whole area of the calf but after the section inhibition could be obtained from the proximal parts of this region.

The inhibitory effects from the ventral side of the limb usually disappeared after severance of adjacent roots. But quite constantly inhibition could still be elicited from certain points near the boundaries of the original excitatory skin area.

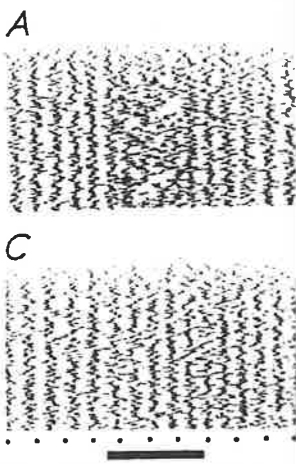
Taken together the results show that excitatory as well as inhibitory effects are conducted in the same dorsal root that supplies the extensor muscles studied. But since the principal part of the excitatory area remained while only small remnants of the inhibitory region were left after severance of all lower roots but S1 it can be concluded that the excitatory inflow is chiefly restricted to the same segment (S1) as the muscle supply while inhibitory impulses predominantly are conducted in other dorsal roots.

It is of some interest that certain excitatory skin points by the section were changed into inhibitory ones and that the excitatory effect from other points presumably was increased by the same procedure. These results must be interpreted to indicate that at least from some points of the skin inhibitory and excitatory influences are intermingled and that the actual effect obtained from these points is a matter of balance between opposite actions.

b. In the experiments described the dorsal root S1 was left intact and the adjacent roots were cut. The problem, however, can also be treated in the opposite way: by cutting the dorsal root S1 and leaving the others intact. But since in the animals used the ankle extensors were innervated by S1 the monosynaptic method could naturally not be used for the investigations.

In some experiments most of the peripheral innervation of the skin was left intact but the musculature of the limb denervated. Recording electrodes were attached to the central stump of the nerve of the ankle extensors in which spontaneous activity was seen. By pinching certain points of the skin of the limb an increase or a decrease of this activity could be obtained but the method of testing was too insensitive for detailed mapping of the limb.

In Fig. 19 A is shown the increase of the activity obtained by pinching the skin over the heel. An inhibition was evoked from the middle part of the plantar region (B). After severance of the dorsal root S1 the conditions changed (below). The excitatory



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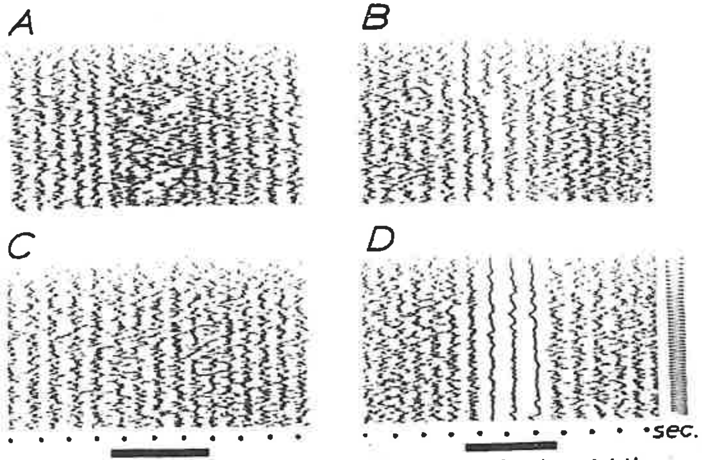


Skin pinched, region over the heel.

Skin pinched, middle part of the plantar region.

Fig. 19. Decerebrated cat. Electrical activity recorded from the nerve of the ankle extensors before *(above)* and after *(below)* cutting the dorsal root S1. After cutting the excitatory effect from the skin over the heel has disappeared (C) but the inhibitory effect from the skin over the middle part of the plantar region has increased (D). Time in msec. (on the right).

effect from the region over the heel disappeared (C) but the strength of the inhibitory influence from the middle part of the plantar region was increased (D).

It is concluded that in this experiment the region over the heel as well as the middle part of the plantar region were innervated by S1, which is the root chiefly responsible for the excitatory effects upon the extensor muscles of the ankle. But the overlap of adjacent roots is great, and so, in the middle part of the plantar region, the inhibitory influence of these roots was strong enough to overcompensate for the excitatory influence of S1. This therefore was concealed. When S1 was severed the concealed excitatory inflow disappeared and thus the inhibition appeared to be increased.

c. Recently the segmental origin of different cutaneous nerves of the limb has been thoroughly re-investigated by Widén (1951). It was shown that the sural nerve and the posterior femoral cutaneous nerve could be mainly referred to the dorsal roots S1 and L7 while the saphenous nerve could be mainly referred to L6 and L5. In the previous chapter it was pointed out that excitation of the ankle extensors is more easily obtained from the sural than from the saphenous nerve (p. 16 and 20).

It is obvious that these findings fall well in line with the statement that the excitatory influences upon the ankle extensors are chiefly conducted in S1. An experiment which clearly elucidates this fact is presented in Fig. 20.

A spinal animal was used and the test shocks were applied to the medial gastrocnemius nerve. The monosynaptic responses were restricted to the ventral root S1. Four cutaneous nerves of the limb were prepared to be stimulated by the conditioning shock and the effects from each of them were read off in the extensor nucleus. At the end of the experiment the dorsal roots were cut and by recording from their distal stumps it could be found to which segments the cutaneous nerves were restricted.

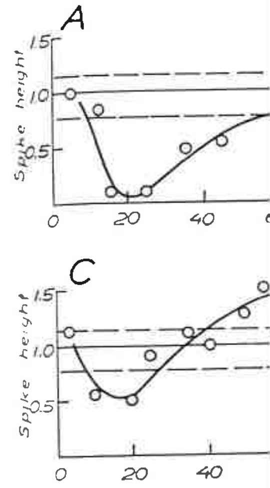
The fibular femoral cutaneous nerve which runs on the ventrolateral side of the thigh was referred to the dorsal root L5. When the conditioning shock was applied to this nerve a marked inhibition was obtained in the gastrocnemius motoneurones (A). There was no late facilitatory effect to be seen.

In Fig. 20 B are shown the excitability changes evoked from the saphenous nerve (mainly entering through the dorsal root L6 but to a smaller degree also through L7). Also from this nerve an inhibition was obtained but it was followed by a weak excitatory phase.

The sural nerve was then stimulated. The afferent volley from this nerve was conducted in the dorsal root S1. The reflex effect of the volley is presented down to the left (C). There was an early inhibition which after about 35 msec. turned into a rather marked facilitation.

Finally the conditioning shock was applied to the posterior femoral cutaneous nerve the afferent volley of which was also conducted in S1. From this nerve no inhibition was obtained. Only an excitatory effect could be seen (D).

It is evident that excitatory effects were most easily obtained from the skin nerves entering through the dorsal root S1 to



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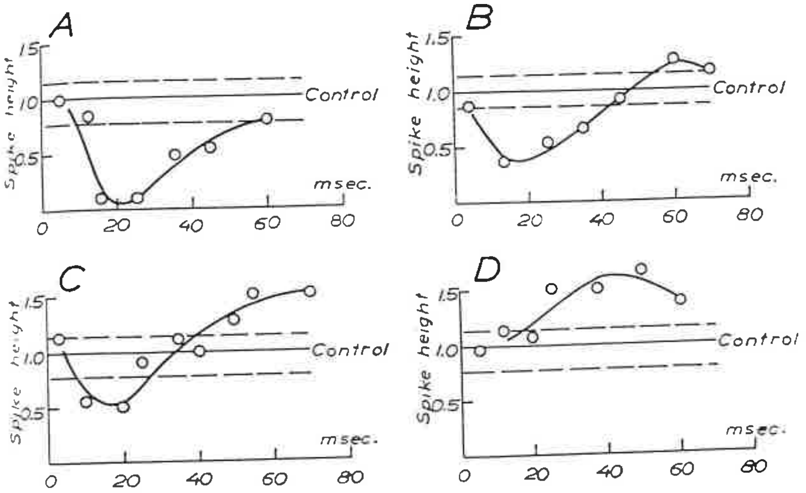

Fig. 20. Spinal animal. Excitability changes in the motoneurones of gastrocnemius medialis following conditioning stimulation of different skin nerves of the limb. See text.

which the afferent supply of the extensor muscle belonged. But the results must not be interpreted to indicate that the fibular femoral cutaneous nerve is "purely" inhibitory and the posterior femoral cutaneous nerve "purely" excitatory to the extensor motoneurones. In many experiments it has been observed that inhibition as well as facilitation could be obtained from both these nerves. It is not the actual shape of each separate curve that is of interest in the experiment described; it is the dominating effects from the different skin nerves that should be compared.

It has been shown that an excitatory effect obtained from a certain point of the skin can be mixed with concealed inhibitory components (*a*) and that similarly in an inhibitory skin area excitatory components can be concealed (*b*). It is also evident that inhibitory and excitatory components seem to be intermingled in all cutaneous nerve trunks of the limb; it is only the relative strength of these two components that varies (*c*).

In the light of these findings some experiments can be explained, the exceptional results of which originally seemed difficult to interpret. One of these experiments was performed on a decerebrated animal with a very pronounced extensor tonus. At first monosynaptic reflexes were elicited from the nerve of the ankle extensors and the skin of the limb was pinched in order to map excitatory and inhibitory skin areas. But from no point of the limb could inhibition be obtained; the only effect was facilitation. The excitatory skin area, however, was not restricted in the usual way to the calf; it extended down to the toes and also to the ventral aspect of the leg.

Then the extensor muscles of the knee were tested and similar results were obtained. Excitatory effects could be evoked not only from the ventral aspect of the thigh but also from the leg and the upper aspect of the foot.

Different results were obtained in another experiment in which a spinal animal was used. In this cat the extensor muscles of the ankle could not be excited from any point of the skin. From the region over the heel there were no visible effects at all but higher up on the calf inhibitory skin points were found. From the foot and the ventral side of the limb marked inhibition was obtained.

These solitary exceptional findings are of particular interest. It is obvious that the existence of excitatory and inhibitory skin areas must not be interpreted to signify that from each point of the skin under all conditions only one effect is obtained. On the contrary, it is evident that most points of the skin under appropriate conditions are capable of changing their reflex functions. Undoubtedly these phenomena can be attributed to the mixed character of the afferent inflow. It is concluded that most points of the skin possess both excitatory and inhibitory spinal connexions to a certain muscle. From the points of an excitatory skin area the excitatory connexions dominate; for an inhibitory skin area the reverse holds true. The final reflex response, however, is not only determined by the character of the afferent inflow, it is also modified by the state of excitability in the spinal cord itself. According to the actual state of balance in the spinal centres either kind of influence is more favoured than the other. A mixed afferent inflow need not therefore always yield the same final response.

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excitatory effects from the skin upon the extensor muscles of the ankle are primarily conducted through the dorsal root S1 but to a certain degree adjacent roots also conduct excitation. Similarly, inhibitory effects upon these muscles are partly conducted in S1 even if the adjacent roots are the ones primarily responsible for inhibition. The dorsal root S1 which is mainly excitatory on the calf muscles also supplies the extensor muscles themselves. The significance of this fact cannot be discussed until it is known whether a similar segmental distribution also characterizes other muscles of the limb.

It has been stated that the excitatory inflow from the skin upon the extensor muscles of the ankle is mainly entering through the dorsal root S1. But the excitatory skin area of the ankle extensors coincides with the inhibitory skin area of tibialis anterior. Thus it seems probable that the inhibitory impulses from the skin upon this muscle are also mainly conducted in the dorsal root S1. The nerve supply, however, of tibialis anterior is usually restricted to L7. The following experiment was planned to elucidate this question.

The monosynaptic method was used to map the inhibitory skin area of tibialis anterior (test reflexes recorded from the ventral root L7). Then the dorsal root S1 was cut, and afterwards inhibition from the skin was no more obtainable.

The extensor muscles of the knee are usually supplied by the dorsal root L6. Their excitatory skin area is mainly localized to the ventral aspect of the thigh. This skin field does not correspond very well with the dermatome of L6, as described by KLESSENS (1914). By appropriate root sectioning it was found that the excitatory influences from the ventral aspect of the thigh were chiefly conducted in the adjacent roots L5 and L4.

A cutaneous nerve trunk from which excitatory effects upon the knee extensors are easily obtained was found to be the saphenous (p. 17 and 20). Similarly, excitation can easily be evoked from the fibular femoral cutaneous nerve, which enters mainly through the dorsal root L5.

Thus as far as the extensor muscles of the knee are concerned, there is no justification for the statement that the excitatory effects from the skin would mainly be conducted in the dorsal root that supplies the muscles themselves.

The semitendinosus muscle is usually innervated by the dorsal root L7 or S1. These roots, however, do not partake in the sensory supply of the inhibitory skin area on the ventral aspect of the thigh (Klessens). The inhibitory inflow from the skin upon this flexor muscle must be mainly entering through dorsal roots other than those innervating the muscle itself.

The excitatory skin area of the extensor brevis digitorum is chiefly localized on the upper aspect of the foot. The muscle itself is usually innervated by the dorsal root L7.

According to Klessens the upper aspect of the foot belongs chiefly to the dermatomes of L5, L6 and L7.

In one experiment the excitatory skin area was mapped before and after severance of the dorsal roots L5 and L6 and it was found that the section almost eliminated the excitatory effects from the upper aspect of the foot.

Thus it is evident that the excitatory effects from the skin upon the extensor muscle of the toes are mainly conducted in dorsal roots which are different from the one supplying the muscle itself.

The flexor brevis digitorum is usually innervated by the dorsal root S1 or S2. It is obvious, however, that the upper aspect of the foot, which constitutes the main inhibitory skin area for this muscle, is not innervated by these roots.

Consequently it is concluded that the dorsal root distribution of skin afferents with different reflex effects upon a certain muscle is not specifically correlated with the segmental supply of this muscle. The fact that the extensor muscles of the ankle are innervated by the dorsal root mainly responsible for the excitatory influences from the skin upon these muscles is not attributable to a general rule. On the contrary, it seems to be mere coincidence.

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DISCUSSION

It has been shown that the actual appearance of excitatory and inhibitory skin areas does not correspond to a strict segmental organization. It is true that excitatory and inhibitory afferents are not evenly distributed to different dorsal roots. Either type is more represented in certain roots than in others. But there is no specific correlation between this type of segmental distribution of skin afferents and the segmental supply of the muscle investigated.

The principles of organization, found in the present investigation, concern the localization of the skin areas. All extensor muscles studied were inhibited from the main part of the limb. But each of them was excited from the skin area localized mainly over the muscle itself. As for the flexor muscles, they were all excited from the main part of the limb, but each of them was inhibited from the skin area localized mainly over the antagonist extensor muscle. This means that all muscles, flexors as well as extensors, are excited when the skin area over the muscle itself is stimulated.

The common notion of the flexor reflex must be re-considered in the light of these facts. It is true that from all points of the limb an ipsilateral movement can be evoked consisting of flexion in most joints of the limb. But if the stimulus happens to fall within a skin area covering an extensor muscle then this muscle contracts, and since this mechanism is reciprocal with respect to the antagonist flexor (inhibition) an extension is evoked at the joint upon which these muscles are acting. The movement at this particular joint will thus diverge from the general flexion pattern that is obtained in all other joints of the limb.

This singular reflex coordination of skin and musculature of the limb can be interpreted in different ways. The local contraction of the muscle under the skin point stimulated might possibly be regarded as a mechanism akin to what is known as "defense musculaire". The contraction of the muscle and the ensuing movement renders the skin over the muscle lax, so that a sharp object will penetrate less readily. Besides, the muscle itself becomes stiff and thus better adjusted to protect underlying tissues. But evidently the movement itself can also be protective.

A withdrawal reaction need not necessarily consist of a flexion movement. If an irritating object comes in contact with the skin over the heel, a flexion of the ankle need not be helpful. An extension of this joint would be better adapted to remove the heel from the ground away from the offending object.

Some of the results obtained above deserve further consideration. It was indicated that the reflex effects from different skin areas must be regarded as a matter of balance between excitatory and inhibitory influences. It has been stated that in a spinal animal excitation can be evoked from a certain point of the skin of the underlying muscle. But this does not signify that the skin point investigated does not possess any inhibitory spinal connexions to this muscle. It only shows that the excitatory connexions dominate. There is thus on the surface of the skin great overlapping between excitatory and inhibitory supply. If, for instance, in one way or another the dominating effects from an excitatory skin area are blocked or sufficiently suppressed, then concealed inhibition may become manifest.

The results suggest that further analysis of the organization of skin reflexes must be based on afferent selectivation. But since sensory units with widely different reflex functions are intermingled not only in the cutaneous nerve trunks and in the dorsal roots but obviously also in the afferent supply of a single skin-point—in the less strict geometrical sense used above—it is difficult to obtain a strictly selective stimulation. In order definitely to solve this problem it will perhaps be necessary to use single fibre preparations.

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GENERAL COMMENTS

The organization of spinal skin reflexes that has been elucidated above throws new light upon an old problem and represents an important field for further investigations. It demonstrates the presence of a set of rules other than the classical one of ipsilateral flexion and thereby assembles under a single heading a number of disconnected observations on ipsilateral extension. The experiments have also drawn attention to the extreme complexity of afferent skin nerves regarded from the point of view of their reflex effects. They have emphasized a connexion between source and centre at the expense of fibre size and centre.

Ipsilateral reflex effects only have been studied in this paper. It would be of great interest also to carry out a detailed analysis of how the musculature of the limb is influenced from different skin areas of the contralateral limb. There is reason to assume that the localization of the skin stimulus is an important factor not only when ipsilateral but also when crossed skin reflexes are concerned.

From the clinical point of view the observations described are of interest. Naturally, animal experiments cannot be directly applied to man but the results obtained in this paper undoubtedly suggest new possibilities for interpreting the mechanism and understanding the significance of the cutaneous reflexes as used in the clinic.

SUMMARY

In decerebrated and spinal cats ipsilateral reflex motor responses were elicited from the skin of the hind limb. The reflex effects were measured either by monosynaptic testing or by myography. Six limb muscles, working in antagonistic pairs upon respectively knee-, ankle- and toe-joints, were studied individually. The conditioning impulses were set up by either electrical or thermal stimulation of the exposed skin nerves, or by adequate means from the skin end-organs.

1. *Electrical conditioning.* By an electrical conditioning shock to a peripheral skin nerve it proved possible to elicit not only inhibition (flexor reflex) but also facilitation of ipsilateral extensor motoneurones. The effect obtained varied with the anatomical localization of the skin nerve conditioned. Certain skin nerves gave dominating inhibition, others dominating facilitation of the extensor nucleus tested. A certain amount of selectivation of these effects could be obtained by choosing different branches of a cutaneous trunk. Both excitation and inhibition were of the reciprocal type.

The effect obtained from a certain skin nerve was different for different limb extensors. Dominating inhibition of a given extensor nucleus was combined with definite facilitation of another. Thus excitation of the extensor calf muscles was more readily obtained from the sural nerve (running over the calf) than from the sapheneous (running on the ventromedial side of thigh and leg); but for the extensor muscles of the knee the reverse held good.

Sometimes the latency of the extensor facilitation did not exceed 4 msec. which indicates that the fastest fibres of the cutaneous nerve were concerned.

2. *Thermal conditioning.* For specific analysis of the reflex function of the small skin fibres they were selectively stimulated by local heating of the cutaneous nerve. It turned out that the reflex effect of the smaller fibres was similar to the effect of the

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large ones. Functional discrimination with respect to reflex effects could not therefore be based on fibre size. Since the effects proved to be related to the anatomical localization of the skin nerve stimulated, adequate stimulation of different skin areas was applied.

3. *Adequate stimulation.* The findings with electrical and thermal stimulation were confirmed and appeared in new light when it was demonstrated that, for both flexor and extensor muscles, specific excitatory and inhibitory skin areas could be mapped out. Each of the extensor muscles studied was inhibited from most parts of the limb but excited from a skin area mainly localized over the muscle itself. Each of the flexor muscles was excited from most parts of the limb but inhibited from a skin area mainly localized over the antagonistic extensor muscle. Thus it cannot be maintained that ipsilateral skin afferents evoke flexor excitation and extensor inhibition. Afferents derived from a skin area covering a certain extensor muscle will, on the contrary, elicit contraction of this muscle and reciprocal inhibition of its antagonist flexor.

The effects were most easily evoked by noxious stimulation of the skin but sometimes similar effects could be obtained also by tactile stimulation of the skin surface. In the same way as the reflex effects were similar for large and small skin fibres so also were they qualitatively similar for different kinds of adequate skin stimuli.

There was no specific correlation between the different skin areas described and the peripheral skin fields of the cutaneous nerve trunks. Cutaneous afferents from different skin areas are intermingled in the same nerve stem. Therefore when stimulating cutaneous nerve trunks, sensory components with very different reflex functions are indiscriminately activated. In accordance with the localization of the skin field, the proportion between inhibitory and excitatory components (for a given muscle) varies for different nerves of the limb.

4. *Segmental distribution.* By comparing the distribution of excitatory and inhibitory skin areas before and after section of the appropriate dorsal roots it was found that the central representation of these skin areas does not correspond to any specific segmental organization of the skin afferents. In the dorsal roots

cutaneous sensory components with different reflex effects are intermingled, just as in the cutaneous nerve trunks.

The experiments on root section also showed that an excitatory effect obtained from a certain point on the skin may be mixed with concealed inhibitory components and that, similarly, in an inhibitory skin area excitatory components may be concealed. Thus the final reflex effect obtained from a certain skin area represents a pattern in which both excitation and inhibition occur even though either effect often is concealed and the other one therefore appears to be relatively pure.

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