

REFLEX ACTIVITY IN CHRONIC SPINAL CATS

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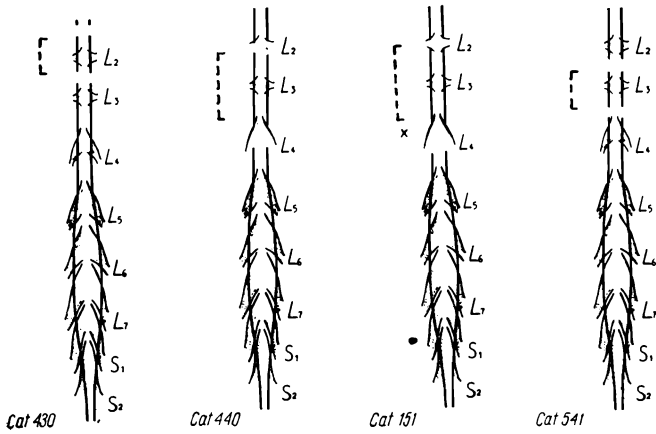
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Reflex activity of spinal mammals have been investigated mostly in acute spinal cats, or in chronic cats and dogs spinalized in the early postnatal stage and tested after various periods (Grayson and Mc Couch 1947, Shurrager and Dykman 1951, Kozak et al. 1962). The amount of data, concerning adult chronic spinal preparations, i.e. operated when the spinal cord has reached maturity, is very scarce and limited almost exclusively to dogs (Goltz and Ewald 1896, Nesmeyanova 1955, 1957, 1959) and semi-chronic cats (Liddell 1934, McCouch et al. 1935, Kellog et al. 1947). This was probably due to the fact that it is fairly difficult to keep adult chronic cats in a good condition after spinalization.

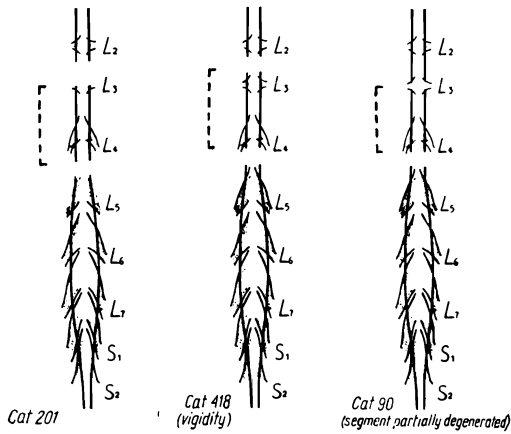
Since the spinal cord of kittens differs anatomically and functionally from that of an adult cat (Langworthy 1929, Skoglund 1960abcd), and since the isolation of structures before they reach a certain degree of maturity may change their specificity (Gelfan 1964), the aim of the present paper was to make a survey of spinal reflexes in adult spinal cats which would allow a comparison with results of experiments on acute spinal cats.

MATERIAL AND METHODS

The experiments were performed on 1.5—2 year old cats spinalized at the lumbar level. In all the animals the spinal cord was divided twice, both transections being separated by 1—2 segments. This was done in order to diminish the effects of sprouting within the spinal cord (Weddell et al. 1941). In most animals the upper lesion was situated at the level of L₂ or L₃, the lower at L₃ or L₄ respectively (Fig. 1A). Only in four cats was the upper lesion done at the level of L₄, whereas the lower was at L₆ or L₇ (Fig. 1B). The spinalization was performed with Nembutal anesthesia under aseptic conditions. Both lesions were made during the same



A



B

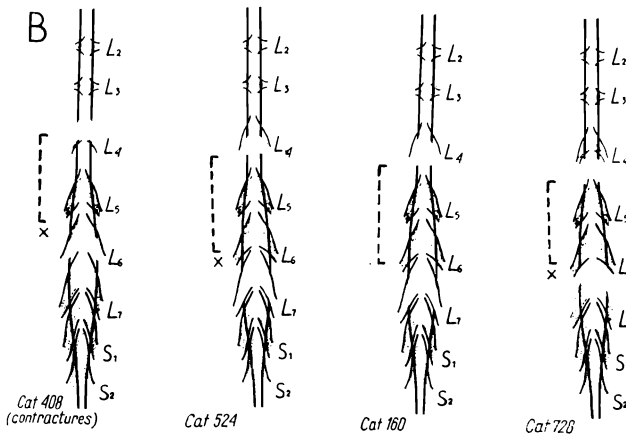


Fig. 1. Diagrams of the spinal cords of the individual cats. A, The animals with the level of transections which isolated segments between L_1 to L_4 . B, The animals with the level of transections which isolated segments between L_4 to L_7 . Incomplete transections are designed by x. Isolated segments are marked by dashed lines

operative session. The present paper includes only those cats (11 animals) in which postoperative recovery was satisfactory, no secondary changes (such as injury of the skin, pathological conditions of internal organs) were observed, and histological control showed that the upper section of the spinal cord was complete. The details of the surgical technique, postoperative care and anatomical analysis of the effects of spinalization will be described in a separate paper (Afelt, in preparation).

The main investigation was done between the 3rd and 5th months after surgery. In addition, in some cats a number of reflexes were also tested earlier between the second and the sixth week, and also later during the 9th and 10th months after spinalization. First, in each animal the assembly of reflexes characteristic for the given spinal cat was examined and defined, whereas later the functional properties of selected reflexes were thoroughly studied under unrestrained conditions. Special care was taken to accustom the animals to the experimental procedure and to test the reflexes on quiet and relaxed animals.

The following reflexes of the hind limb were studied: flexion, extension, rotation of the foot, toe-fanning, toe-extensor reflex, grasping reflex, bilateral extension, crossed extension, bilateral flexion and stepping reflex. The results concern mainly reflexes evoked from the skin of the lower part of the leg and perianal region, which are innervated exclusively by afferents entering the spinal cord below the level of its section. In some spinal cats the skin of the thigh preserved cutaneous sensitivity, which shows that it was partly innervated from levels above the section.

Stimuli were classified in relation to their physiological properties (Adrian and Zotterman 1926ab, Zottermann 1939, Wall 1960, Loevenstein 1961, Weddell and Miller 1962, Iggo 1966, Burgess et al. 1968, Perl 1968), and the type of reflexes elicited by them. The applied stimuli were as follows:

1) pure tactile stimuli: (a) bending of a few hairs, (b) single stroke of a small brush not touching the surface of the skin, (c) several successive stroking applied in the direction opposite to that of hair growth, without touching the skin;

2) tactile-pressure stimuli, all of them evoking small, visible deformation of the skin: (a) air-puff, (b) Frey's hairs with 1 and 5 g of pressure force, (c) weak squeezing with fingers;

3) pressure stimuli: (a) pressure with a blunt needle point, (b) slight pressure exerted on the whole surface of the central pad, (c) pressure exerted on large skin areas;

4) nociceptive stimuli: (a) weak pinching with thin tweezers, (b) pinprick, (c) strong pinching, (d) affixing a clip (rarely, in order to prevent mechanical injuries);

5) others stimuli: (a) pressure of the central pad forward of the heel, (b) simultaneous pressure on the toe pads, (c) rubbing the skin, (d) cooling with either a drop or a fine squirt of ethyl chloride administered for 1 sec, (e) tapping and pressure with blunt object along a straight line over particular muscles.

Different stimuli were applied to the same areas of the skin and their effects were examined in respect to different type of reflex response.

In order to have relatively uniform experimental conditions the number of variables in the experiment was limited to a minimum. To prevent adaptation and fatigue only 1 to 3 identical trials (i.e. application of the same stimulus to the same area) were applied in a single experimental session. One experimental session consisted of a maximum of 10 trials, with intertrial intervals of at least 2 min. This appeared to be especially important in reflexes elicited from skin covering

particular muscles and also to some extent for toe-fanning and the toe extensor reflexes. In other reflexes the adaptation and fatigue did not appear to be an essential factor. The animals were tested once every few days and the same tests were repeated after a few weeks. In this way both the habituation of reflexes and the effect of "spreading activity on already active muscle" (Dimi-trijevič and Nathan 1968) were eliminated. The place stimulated was considered as the receptive field of a given reflex if at least five identical responses were evoked by the same stimulus.

The experiments were performed on cats in the following two positions: (i) the animal lying unrestrained on one side with both hind limbs flaccid in a slightly flexed position, and (ii) the animal lying half-restrained in a special stand in which the hind part of the body was hanging down passively, the hind limbs having no support. In such a situation there was slight tension in the extensor muscles. Some kinds of reflexes were also investigated in the passively flexed and passively extended leg. The reflexes evoked when the animal actively contracted the muscles of the back have been not included in this paper. Similarly, the reflexes which can be evoked from skin areas with small temporary injuries and from the permanently wet region of the anus and genitals were eliminated. The results from cats exhibiting rigidity in different joints were included in the material, although they were given separate consideration.

The animals were sacrificed 5 to 11 months after surgery. The spinal cord was removed and photographed for verification of the level of sections. The material was fixed in 10 per cent neutral formalin. The lumbo-sacral part of the spinal cord was divided into two or three blocks, and embedded in paraffin. Serial sections 10 μ thick were made in the frontal plane. The preparations were stained with Nissl and Klüver-Barrera methods and some by the Weil method. The transection of the spinal cord was considered as complete, when no fibers passing through the scar tissue were found.

RESULTS

Ipsilateral hind limb reflexes

Reflexes from skin covering particular muscles. The surface of the skin on the cat's hind limb was divided into the following regions which are schematically marked in Fig. 2: (a) over fascia lata, (b) over m. biceps femoris, (c) over m. semitendinosus, semimembranosus, gracilis, (d) over m. tibialis anterior, (e) over m. gastrocnemius, flexor digitorum longus, flexor hallucis longus, (f) over m. peronei and extensor digitorum longus, (g) plantar aspect of shank, (h) dorsal aspect of shank, (i) lateral aspect of shank over digit V, (k) medial aspect of shank over m. interosseus digiti II.

Stimulation of the skin covering extensors, and of the plantar aspect of the shank (Fig. 2ceg, and 3) by bending the hairs and stroking them, especially in the opposite direction to their growth, was ineffective or else evoked a response in the form of a slow extension of the leg in the knee, ankle or all joints together. This happened mostly when the area of

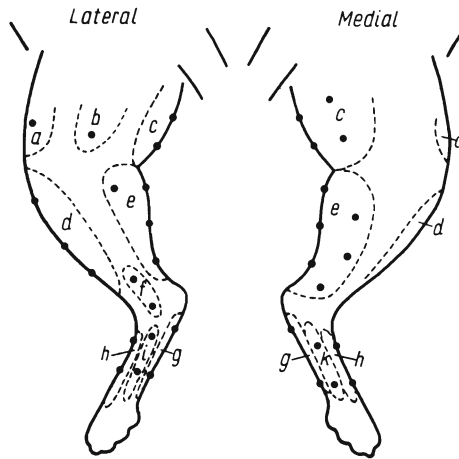


Fig. 2. Scheme of the skin regions under investigations. Particular fields were delineated by dashed lines. Dots represent points of local stimulation (pinching, air-puff etc.). a, skin over fascia lata, b, skin over m. biceps femoris, c, skin over m. semitendinosus, semimembranosus, gracilis, d, skin over m. tibialis anterior, e, skin over m. gastrocnemius, flexor digitorum longus, flexor hallucis longus, f, skin over m. peronei and extensor digitorum longus, g, plantar aspect of shank, h, dorsal aspect of shank, i, lateral aspect of shank over digit V, k, medial aspect of shank over m. interosseus digiti II

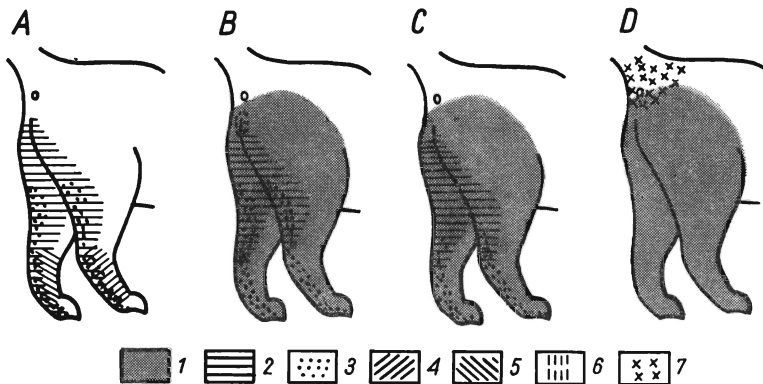


Fig. 3. Spinal reflex fields in relation to different kind of stimulation. A, pure tactile stimulation — bending a few hairs and stroking without touching the skin, B, weak tactile-pressure stimulation — air-puff, C, mixed stimulation — weak pinching, D, nociceptive stimulation and cooling — strong pinching, affixing of a clips, cooling with ethyl chloride. Symbols: 1, flexion (general or of particular flexors), 2 extension (general or of particular extensors), 3, toe fanning, 4, rotation of the foot with heel abducted, 5, rotation of the foot with heel adducted, 6, bilateral extension, 7, stepping reflex

the skin stimulated was fairly large. The application of a single stimulus evoked responses only in some cats, whereas repetitive stimulation was effective in most animals. The air-puff and weak nociceptive stimuli evoked either extension similarly to tactile stimuli or a flexion of the leg, e.g. weak pinching the skin covering m. gastrocnemius evoked either knee flexion and at the same time extension of the ankle, or an extension of the whole leg, and only rarely, general flexion in all joints. The air-puff was not very effective and in most trials did not evoke any responses. Weak nociceptive stimuli evoked responses in almost all trials. Somewhat stronger nociceptive stimuli and sudden cooling always caused flexion of the stimulated leg.

The extension evoked by air-puff stimulation appeared more frequently when the cat was hanging than when it was resting relaxed on one side. When the distal part of the leg was stimulated, the extension was combined with toe-fanning (see below).

Stimulation of the skin covering flexors and the dorsal aspect of the shank (Fig. 2bdfh and 3) by bending the hairs and stroking them did not yield any reaction. All the other stimuli produced flexion. Sometimes, and in particular when the air-puff was used, it produced a local reflex (e.g. stimulation over m. tibialis anterior elicited flexion at the ankle), in other cases, especially when nociceptive stimuli were applied, the flexion reflex was generalized. The weaker the stimulus, the less frequently were the responses obtained. After the application of sudden cooling and strong nociceptive stimuli, the flexion was followed by several other more generalized movements for instance by repetitive attempts to shake off the stimulating agent, though the stimulation was discontinued.

Tapping of particular muscles evoked a response from the given muscle. For example tapping (through the skin) m. tibialis anterior evoked ankle flexion followed by slow general leg flexion. Tapping of the m. gastrocnemius evoked extension of the ankle followed by slow extension of the whole leg. Tapping of the m. flexor digitorum longus evoked the slow extension of the leg etc.

Rotation of the foot with abduction or adduction of heel. Stimulation of the lateral part of the shank (Fig. 2i, and 3) evoked a lateral movement so that the foot took a position with the plantar surface facing laterally, and the heel abducted. Stimulation of the medial part of the shank (Fig. 2k, and 3) evoked the opposite movement. The boundary between the receptive fields of these two reflexes runs through the middle of the dorsal and plantar parts of the shank. In both cases the most effective stimuli appeared to be stroking with a brush, especially if repetitive stimulation of large skin areas was used. Pressure and nociceptive

stimuli were frequently ineffective. In most spinal cats these reflexes were evoked only from the distal part of the shank. Long lasting tactile stimulation evoked sometimes different reflexes simultaneously, for example, toe fanning and lateral rotation of the foot could be evoked from the latero-plantar part of the shank.

Toe-fanning. Dorsiflexion and spreading of the toes — the toe fanning reflex (Fig. 4) was evoked most frequently by bending the long hairs projecting between the toes, and by stroking with a brush the hairy skin on the ventral part of the foot. Repetitive stroking applied to the plantar area of the shank in the opposite direction to the hair growth,

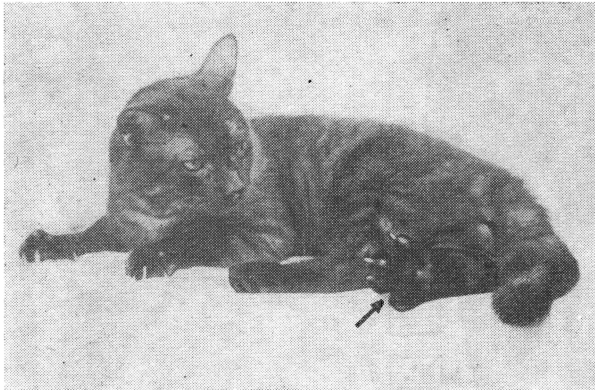


Fig. 4. The toe-extensor reflex. The arrow indicates the place of stimulus applied

also evoked this reflex. Similar results were observed when rubbing, weak pinching and cooling were applied (see also Kozak and Westerman 1965). On the other hand strong nociceptive stimulation applied to the same skin areas evoked a general flexion of the leg, usually without any movements of the toes.

The toe-fanning appeared usually combined with other reactions, except when using, weak stimulation of the hairy skin on the ventral part of the foot, which in most animals could evoke isolated toe fanning. More often it was combined with knee and ankle extension especially to moving the hairs. The same stimulation of the shank nearly always evoked such an assembly of reflexes, whereas the same stimulation of the skin covering extensors of the ankle only sometimes yielded toe fanning (see above). The receptive field of the reflex is schematically marked in Fig. 5. The application of such stimuli as rubbing and, sometimes, pinching could evoke toe fanning combined with either extension or a general flexion of the leg. However, in most animals the occurrence of the flexion reflex, passive flexion of the leg, or pressure exerted on a large skin area caused toe-fanning to become

less regular, with higher threshold and in some instance it did not occur at all. On the contrary, passive extension of the leg facilitated the toe fanning especially in cats in which all the reflexes had high thresholds. In the cats exhibiting rigidity the threshold of toe fanning was very low and, sometimes, moving of one hair could evoke the reflex. Ethyl chloride applied to the receptive field of the toe fanning reflex evoked in all cases a rapid but weak flexion followed by toe fanning and extension of the whole leg and, frequently, also "shaking off". In some spinal cats toe fanning was evoked by tapping the foot dorsum.

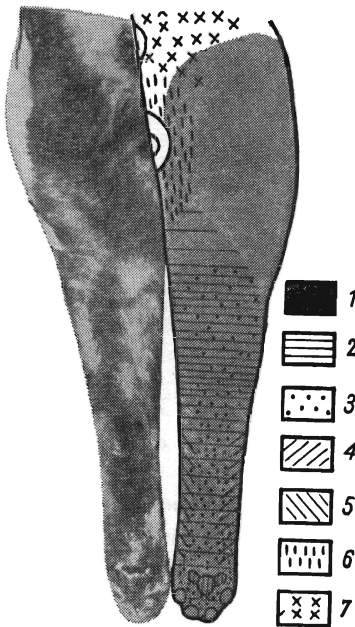


Fig. 5. Map of the receptive fields of various reflexes. Symbols are the same as in Fig. 3

Reflexes of plantar flexion of toes. A plantar flexion of the toes was evoked by stimulation of the central pad, and in particular its medial and anteromedial parts (Fig. 5). It did not involve any movement of the claws. The effective stimuli were touch with Frey's hairs, local pressure with a blunt needle point, pressure over the whole central pad and squeezing with fingers. Stimulation of a larger surface was less effective than the local deformation of more superficial structures. The reaction is in fact the toe extensor reflex (Engberg 1964ab). Squeezing with fingers or weak pinching of the plantar cushion evoked in addition to the toe extensor reflex a general flexion reflex. Strong pinching and other strong nociceptive stimuli elicited only a general flexion reflex. The toe extensor reflex could be evoked in a passively extended

leg. In some cats this reflex had a high threshold or did not appear at all. This seemed to be independent of the level of spinalization or degree of rigidity.

A plantar flexion in the basal and middle phalanx with protrusion of claws, i.e. grasping reflex (Cohen and Iannone 1967) was elicited by touching and pressing (toward the heel) of the central pad with a simultaneous passive dorsiflexion of toes, evoked, for example by pressure on the pads of toes. Pressure over the area between the central and the toe pads was also very effective. In most cats the reflex appeared only when the limb stimulated was in flexion, though in some animals it could be evoked also when the limb was passively extended. In those animals in which the threshold of the grasp reflex was high, the response could be facilitated by pressure on large skin areas, or by a special position of the limb. For instance in cats in which rigidity was present, the grasp reflex could be evoked only in the leg which was in contact with the ground (when the cat was lying on one side) and could not be evoked when both the hind limbs were hanging freely.

Bilateral reflexes

A receptive field, which according to Chambers (Chambers et al. 1966) form a ring sweeping from the perianal region around the lateral border of the perineum to the mid-line ventral to the genitals, was stimulated by touch of the skin surface, an air-puff, weak and strong pinching, and cooling with ethyl chloride. In some cats with high level (above L_4) spinal cord transection, the stimulation of the anteromedial part of this field by light touch of the skin surface or an air-puff led to the *bilateral extension* of the hind limbs in all three joints. The remaining stimuli were ineffective in relation to this reflex. In all spinal cats with a low level (below L_4) spinal cord section the bilateral extension reflex could not be evoked.

No *bilateral flexion* from this area was observed in any of the animals to any kind of stimulation.

Stimulation of the perianal region, especially if nociceptive, evoked a *rigid "step"* flexion of the ipsilateral, and crossed extension of the contralateral hip, together with bilateral extension in both knees and ankles. This could be evoked in all low spinal cats and in most animals with a high level transection.

The *crossed extensor reflex* to nociceptive stimulation of the distal part of the leg was obtained only in high spinal cats. The longer after surgery the more difficult it was to obtain this reflex. For example 2—6 weeks after the spinalization it appeared regularly, whereas after 5—10 months rather sporadically. In the latter period the crossed extensor

reflex appeared more frequently when the cat was hanging down than when it rested relaxed on one side.

According to Sherrington (1910) the *hind limb stepping reflex* can be evoked in cervical and thoracic spinal cats by (i) proprioceptive stimuli like passive bilateral extension in hip and knee joints under the limb's own weight, as for instance by lifting the animal from the ground, or by (ii) continuous nociceptive stimulation of the skin outside the limb itself, e.g. of the neck, back, or in the perianal region, or on the tail. In none of the lumbar spinal cats could the hind limb stepping reflex be evoked by proprioceptive stimuli, or nociceptive stimulation of the back. In some of the cats, those with a high level of spinalization, the stepping reflex could, however, be evoked by stimulation of the perineum and tail (Fig. 3 and 5). In such cases the stimulation of various parts of this field was effective in different animals. In some cases cooling yielded results similar to those evoked by strong and continuous nociceptive stimulation, i.e. affixing of a clip. Squeezing also appeared to be an effective stimulus, whereas rubbing of the skin was almost completely ineffective. The possibilities of evoking the stepping reflex diminished with time after the spinalization. For example up to 10 weeks after the spinalization the stepping reflex occurred in most trials whereas after 5 to 10 months it was observed only sporadically. Also, the cutaneous receptive field of stepping diminished with time. In lumbar spinal cats in which rigidity was present the stepping reflex could not be elicited at all.

DISCUSSION

In the present study the lumbo-sacral part of the spinal cord was examined under conditions of complete and longlasting isolation from the higher parts of nervous system.

The spinal cord was transected at various levels in different animals. Due to a relatively low level of spinalization all the reflexes from the back were eliminated, and the total amount of reflexes from the hind limbs diminished. For example the proprioceptively evoked hind limb stepping reflex, and the bilateral flexion reflex were absent, whereas the crossed extension, bilateral extension, and the stepping reflex activated from the skin were preserved partially in cats with a high lumbar (above L₄) transection of the spinal cord. Since these reflexes were not present in cats with the spinal cord transected at a lower level than L₃, their absence might be due to extensive damage of motor nuclei innervating hip muscles, located in the cranial part of the lumbar spinal cord (Romanes 1951, 1964).

The great variations in reflex thresholds between different animals cannot be related to the lack of supraspinal control, because this last was excluded in all animals, but may be related to changes in different reflex paths at the interneuronal level. It may be assumed, that as a result of postoperative changes in the blood supply of particular parts of the spinal cord, different groups of neurones were eliminated, especially some of the interneurons (van Harreveld and Schade 1962). The behavior of the remaining interneurons could be altered due to the reduced number of interconnections, in particular intraspinal ones (Cannon and Rosenblueth 1949, Gelfan 1964). The isolation of the lumbosacral part of the spinal cord cannot be expected to "denervate" the spinal motoneurons (Tower et al. 1941), but we do not know whether or not this also applies to the interneurons. The factors mentioned above may have caused selective changes of each particular reflex arc.

Most of the results presented above concern the ipsilateral reflexes evoked from skin. In the acute spinal animal electrical stimulation evokes as a rule a flexion reflex, whereas ipsilateral extension is revealed only occasionally (Sherrington 1903, Graham Brown and Sherrington 1912, Denny-Brown and Liddell 1928, Ranson and Hinsey 1930, Hagbarth and Naess 1950). As suggested by McCouch (Chambers et al. 1966) natural stimulation could be much more "effective" in this type of experiment, and the same method has been adopted in the present study.

In the chronic spinal cat a sufficiently strong nociceptive stimulation of the skin always caused a general flexor reflex independently of which part of the skin of the leg was stimulated. Weak tactile-pressure stimulation, for example, by air-puff applied to the hairy skin, also elicited the flexion reflex, whereas the latter could not be elicited by a pure tactile stimulation such as moving the hairs. As is known, the activation of nociceptors causes the "protective" reflex (Sherrington 1906). The possibility of evoking the flexion reflex by air-puff stimulation, and the lack of this reaction to moving the hairs seems to point out that weak mechanical stimulation of the small size fibres is sufficient to evoke the flexion reflex in the chronic spinal cats. As shown in electrophysiological studies, moving of the hairs stimulates the low threshold, fast and slow adapting mechanoreceptors (Adrian 1931, Frankenhauser 1949, Cauna 1962, Iggo and Muir 1969), whereas innocuous and quite mild mechanical stimulation may excite the great majority of small myelinated and C fibres (Douglas and Ritchie 1959, Brown and Iggo 1967), which seem to be responsible for the flexion reflex.

In the present experiments extension, toe-fanning, rotation of the foot, and the toe-extensor reflex could not be evoked by strong nocicep-

tive stimulation. The same was observed in the case of the extensor thrust (Sherrington 1903) and of the normal plantar response in man (Grimby 1963). The fact that the touching of single hairs *may* be sufficient for evoking toe-fanning and extension from the skin above extensors, and that stroking of hairs may evoke rotation of the foot suggests that the stimulation of low threshold mechanoreceptors is an appropriate factor for these reflexes. On the other hand, in acute experiments Hagbarth (1952) describes that both in decerebrated and spinal cats, touching the hairs with cotton wool usually failed to elicit any muscular responses.

It may be noted that various weak stimuli "effective" in chronic spinal cats, elicit the orienting and/or specific responses in intact and quite awake cats.

In chronic spinal cats the ipsilateral flexion reflex could be obtained from the whole hind limb, whereas the extension reflex could be elicited only from the skin above extensors. In acute spinal cats the stimulation of the skin over a given muscle facilitates a monosynaptic reflex from this muscle and inhibits the monosynaptic reflex from its antagonists (Hagbarth 1952, Eldred and Hagbarth 1954, Megirian 1962). In the case of flexors, facilitation of their monosynaptic reflexes can be evoked from practically the entire surface of the hind limb of the cat. The areas from which facilitation of flexor and extensor monosynaptic reflexes can be evoked in acute spinal cats correspond very well to the areas from which flexion or extension reflexes could be evoked in chronic spinal cats.

The present results show that the receptive fields of various reflexes may overlap completely or partly (see Fig. 5). In the case of antagonistic reflexes like flexion-extension, the kind of stimulation may decide which of the reflexes will appear. The analysis is more complicated in the case of antagonistic reflexes elicited by a similar kind of stimulation from overlapping receptive fields. For example, tactile stimulation of the plantar part of the shank evoked the toe extensor reflex in acute spinal cats (Engberg 1964ab), whereas in the chronic animals toe fanning has been obtained from this area. This might be due to the fact that in acute spinal cats, as compared with chronic ones, the receptive field of the toe-extensor reflex is larger while that of the toe-fanning is smaller. Another explanation would imply that the plantar part of the shank is receptive field of both these reflexes and the predominance of one of them depends on some other experimental factors than specificity of natural stimuli.

In fact, since a particular skin area may be considered the receptive

field of several different reflexes, various types of stimuli applied to the same area, may elicit a different reflex assembly.

As was noted, the position of the stimulated limb influences the effect of stimulation. For example in most animals the passive extension and rigidity facilitates toe fanning, whereas passive and active flexion to some extent inhibited this reflex. In acute spinal animals the monosynaptic reflex from *m. extensor digitorum brevis* is facilitated from *m. gastrocnemius* and inhibited from *m. tibialis anterior* (Wilson et al. 1960). It might be assumed therefore that the toe fanning and the extension reflex are synergistic, but the toe fanning and general flexion reflex are not antagonistic since they may appear together. Perhaps the toe extensor reflex and the flexion-extension reflexes are reversely related. The analysis is difficult since the toe extensor reflex is an intrinsic part of the more complicated grasping reflex.

The grasping reflex in chronic spinal cats was evoked by simultaneous passive dorsiflexion of toes and pressure of the central pad, and could be facilitated by flexion of the leg. These observations seems to explain the functional significance of some electrophysiological phenomena. For instance, the monosynaptic reflex from *m. flexor digitorum longus* (protrusion of claws) is facilitated by a delicate touch of the central pad (toe extensor reflex), and the motoneurons of *m. flexor digitorum brevis* (toe extensor reflex) are facilitated by the nociceptive stimulation of the toe pads (general leg flexion) (Engberg 1964ab). The monosynaptic reflex from *m. flexor digitorum longus* (protrusion of claws) is inhibited from *m. gastrocnemius* (extension), etc.

The results suggest that further analysis of the organization of ipsilateral skin reflexes must be based on afferent selectivity.

SUMMARY

1. Reflex activity has been studied in adult chronic spinal cats, with spinal cord section at the lumbar level.

2. The following reflexes have been investigated: flexion, extension, toe fanning, toe extensor reflex, rotation of the foot, bilateral extension, crossed extension, bilateral flexion and stepping reflex; they were evoked by different natural stimuli: tactile, pressure, nociceptive and mixed.

3. The receptive field and its adequate stimuli, evoking conditions and synergies with other reactions were analysed for each reflex.

4. The spinal reflexes in chronic preparations versus those in acute preparations were discussed.

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