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SPATIAL PATTERNS OF REFLEX EVOKED BY PRESSURE STIMULATION OF THE FOOT PADS IN CATS

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SUMMARY

1. The spatial patterns of reflexes elicited by localized pressure stimulation of the foot skin were analysed by recording electromyographic activities of various hindlimb muscles or muscle nerve discharges in cats anaesthetized with sodium pentobarbitone.

2. Reflex discharges evoked by stimulation of the central pad occurred mainly in physiological toe extensors located in the foot. Stimulus–response relationships of single motor units revealed characteristically wide ranges of graded response and recruitment.

3. Within the central pad, the strongest excitation was evoked from the central lobe and was distributed to extensors of all four toes. Excitation from the medial and the lateral lobes was usually asymmetrical and weaker in toe muscles of the stimulated side. It is suggested that the weakness was in part due to concomitant inhibition.

4. Stimulation of a toe pad caused marked suppression of central pad-evoked activity of toe extensors with a highly specific spatial pattern. The inhibition was strongest in extensors of its own toe, and gradually weaker in the more distant toes. Weak excitation was occasionally evoked in extensors of the most medial or lateral toes, when the most lateral or the most medial toe-pad, respectively, was stimulated.

5. A similar pattern of reflex to that from the toe pad was evoked from the claw base and the hairy toe dorsum of each digit.

6. Reflex effects, both inhibitory and excitatory, from the central and toe pads, claw bases and toe dorsum were maintained during prolonged stimuli, indicating that slowly adapting receptors contributed to these reflexes.

7. It is concluded that stimulation of localized skin areas of the foot, particularly the pads, evokes highly specialized reflexes, which may be important in controlling movements of individual digits.

INTRODUCTION

Since the classical work of Sherrington (1906*a*, 1910), it has been known that the nature of spinal reflexes evoked from the skin is determined by the locus of the stimulus. For example, the flexion reflex is elicitable from a wide skin area covering the limb and produces motor reactions generally consisting of flexor excitation and extensor inhibition (Sherrington, 1910; Lloyd, 1943; Eccles & Lundberg, 1959*a*), but reflex movements evoked from different areas are not identical (Sherrington, 1910). The influence of the location of a stimulus, or 'local sign' (Sherrington, 1906*a*), is more obvious in some cutaneous reflexes (Sherrington, 1903, 1906*a*, *b*, 1910; Hagbarth, 1952; Engberg, 1964; Egger & Wall, 1971; Pierrot-Deseilligny, Bergego, Katz & Morin, 1981; Pierrot-Deseilligny, Bergego & Katz, 1982). One of the most notable reflexes in this regard is the toe extensor reflex (or the plantar cushion reflex) reported by Engberg (1964) and Egger & Wall (1971). According to these authors, pressure stimuli to the central pad of the cat hindlimb elicit strong plantar flexion of all four toes. This reflex movement is caused by selective contraction of toe extensors, particularly those of the intrinsic foot muscles. Slowly adapting mechanoreceptors in the glabrous skin are considered to be mainly responsible for the reflex. Engberg (1964) proposed that the reflex may function to stabilize the foot during standing and during the stance phase of locomotion.

The importance of the locus of the stimulus is striking in the toe extensor reflex (Engberg, 1964; Egger & Wall, 1971). Thus, pressure stimuli applied to the central pad evoke plantar flexion of the toes but those to the toe pads do not. This, however, does not necessarily indicate that stimulation of the toe pad is not relevant to this particular reflex, but instead might reflect a difference in the pattern of reflex actions between the central and toe pads. Since the cat supports its body weight with both the central and toe pads in contact with the ground, and since both contain homologous mechanoreceptors (Jänig, 1971*b*), it seems likely that afferent information from the toe pads may also play an important role in the control of the toe movements. The present study was therefore undertaken to investigate the input–output organization of reflexes from different areas of the foot glabrous skin, particularly the toe pads. The results show that stimulation of the toe pads indeed evokes distinct reflexes of highly specific patterns, acting differentially on the intrinsic plantar muscles of individual digits. It is proposed that the functional role of reflexes from the glabrous skin is more comprehensible when the effects from the central and the toe pads are considered together. A preliminary account of some of the results has been presented (Hongo, Kudo, Oguni & Yoshida, 1985).

METHODS

Experiments were carried out on fifteen adult cats (2·7–3·5 kg) anaesthetized with sodium pentobarbitone (initial dose 40 mg kg^{-1} I.P., supplemented by 2–5 mg kg^{-1} h^{-1} I.V.). The spinal cord was transected at the 13th thoracic segment. In five experiments the transection was performed during recording to compare reflex actions before and after spinalization. The blood pressure was kept at 100–130 mmHg by administering Ringer solution when necessary, and the rectal temperature was maintained at around 37 °C throughout the experiment.

The electromyographic (EMG) activities in the following intrinsic plantar muscles were recorded routinely: medial and lateral portions of flexor digitorum brevis (FDBm and FDBl), interossei of individual digits (II-, III-, IV- and V-IO; the first digit is lacking in the foot), lumbricales superficiales (LS). These muscles combine to plantarflex the toes, mainly at the metatarsophalangeal joint. The function and anatomy of these muscles have been described (Reighard & Jennings, 1935; Straus & Sprague, 1944; Engberg, 1964). Other hindlimb muscles studied included: lumbricales profundii (LP), flexor digitorum and hallucis longus (FDHL), plantaris (Pl), medial gastrocnemius (MG), lateral gastrocnemius (LG), soleus (Sol), tibialis anterior (TA), extensor digitorum brevis and longus (EDB and EDL), peroneus longus (PerL), peroneus brevis and tertius (PerBT), anterior and posterior part of biceps (AB and PB), semitendinosus (St), semimembranosus (Sm). The intrinsic plantar muscles were approached via a skin incision made along the mid-line of the sole. The tendons of Pl, FDB and FDHL were cut distally to visualize the deeper foot muscles. During recording, the left hindlimb was slightly extended, and the foot was positioned horizontally supported at its dorsum by a small platform. Exposed muscles were prevented from drying by covering with cotton gauze soaked in saline. EMG recordings from small intrinsic foot muscles were made using pairs of 0·1 mm metal wires insulated with enamel except for their very tips. Electrodes were inserted separately into the muscle with their tips 1–3 mm apart. To record from large proximal muscles, pairs of electrodes made of 0·3 mm Teflon-insulated stainless-steel wires, with tips exposed for 2–3 mm, were used. Concentric needle electrodes were used for recording single motor units.

In four animals, the nerves innervating IO of individual digits were dissected and the proximal cut ends were mounted on bipolar silver-wire electrodes for recording discharges of motor fibres. Each nerve consisted of branches of both adductors and abductors of one digit.

The central pad (the plantar cushion or metatarsal pad; CP in Fig. 1*A*) and toe pads (IIP–VP in Fig. 1*A*) were stimulated either manually or with a servo-controlled actuator. Manual stimulation was made by pressing the pads with blunt forceps. The onset, duration and relative magnitude of stimulus were monitored by means of a strain gauge bonded on the forceps. For quantitative analysis, pressure stimuli were applied with flat disc probes (diameters 1–15 mm) attached to the actuator, which could generate a constant force of 0·01–20 N or a constant displacement up to 10 mm. Intervals of 20–30 s were interposed between successive tests.

EMG and nerve activities were fed to differential amplifiers with a bandpass of 50–2000 Hz. For motor-unit analysis, single-unit activities were discriminated, digitized and counted in 0·2 s bins during constant force stimulation. Raw records, output of the counter, and signals from the mechanical stimulator were displayed on a thermosensitive chart recorder (DC–2000 Hz).

RESULTS

Reflexes evoked from the central and toe pads were studied by recording EMG (eleven cats) and nerve discharges (four cats) of hindlimb muscles. In five cats, the reflexes were compared before and after the cord transection at the lower level of the 13th thoracic segment. The transection did not change the pattern of reflexes described below, though the procedure tended to somewhat augment the reflex actions and to decrease mechanical thresholds.

Reflex actions from the central pad

Reflex movements elicited by mechanical stimulation of the central pad (CP) of the foot in cats anaesthetized with sodium pentobarbitone were similar to those observed by Engberg (1964) in unanaesthetized spinalized cats and by Egger & Wall (1971) in cats anaesthetized with allobarbitone (Dial). Thus, pressure stimuli applied to the central pad caused plantar flexion of all four toes. The threshold of mechanical stimuli for eliciting the reflex was much lower than that for the general flexion reflex. The flexion reflex involving flexors of the hip, knee and ankle was often difficult to elicit or absent in our preparations under pentobarbitone anaesthesia.

Muscles involved

Systematic EMG recording from various hindlimb muscles revealed that reflex discharges evoked by stimulation of the central pad occurred mainly in physiological toe extensors that plantarflex the toes (Fig. 1*B*), most prominently in those located in the foot. During the maintained pressure stimuli IO, FDB and LS invariably exhibited intense activity which adapted only slowly. Similar excitation was observed in LP examined in one animal. Responses of Pl and FDHL were much weaker than those of the intrinsic foot muscles (Fig. 1*B*) and were often absent. In some animals very weak reflex activity usually consisting of only a few active units was elicited in PerBT, TA and EDB. Other proximal muscles (MG, LG, Sol, AB, Sm, PerL, PB and St) were not activated. The results obtained in nine cats are summarized in Fig. 1*A*, where strongly (black), weakly (shaded) and not (dotted) excited muscles are indicated. Thus, the output pattern as indicated by EMG discharges in anaesthetized cats was in good agreement with previous observations obtained by monosynaptic reflex testing in unanaesthetized spinal cats (Engberg, 1964).

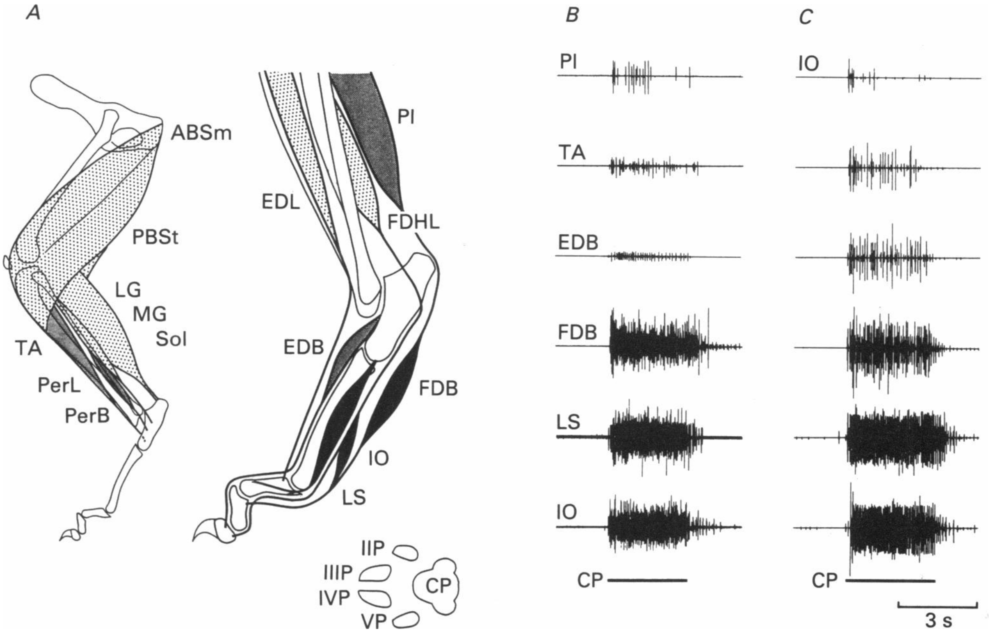

Fig. 1. Responses of hindlimb muscles to pressure stimuli applied to the central pad. *A*, schemata showing the locations and responsiveness of muscles examined, and foot pads. Degree of excitation in each muscle is indicated by the tone of darkness: strong (black), weak (shaded) and no excitation (dotted). *B*, specimen EMG records from various hindlimb muscles. Pressure was applied during the period indicated by the bar in the bottom. Note strong and sustained discharges in toe extensors located in the foot (FDB, LS, IO). *C*, responses of interosseus muscle (IO) to stimuli at different intensities. Pressure was increased from top to bottom.

EMG responses of intrinsic foot muscles

Figure 1*C* shows EMG discharges of IO muscles in response to stimulation of the central pad at different pressures. Note that the stronger the pressure, the more enhanced were the tonic reflex discharges with recruitment of additional motor units.

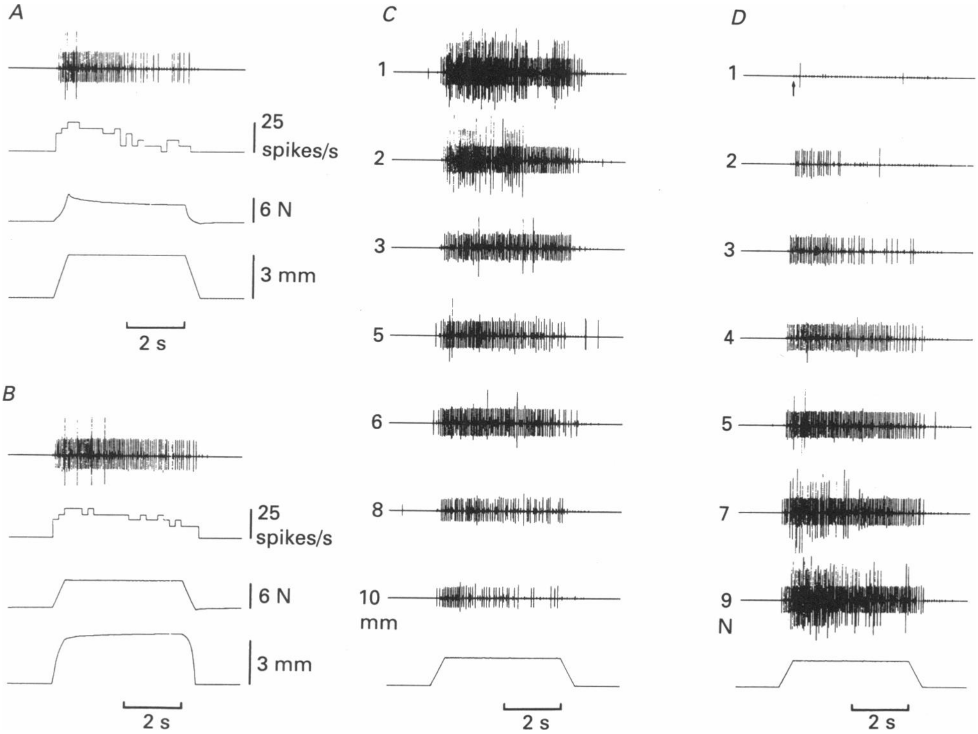

Fig. 2. Responses of single motor units to mechanical stimulation of the central pad. *A* and *B*, time course of discharges of FDB units during constant displacement (*A*) and constant force (*B*) applied with a 6 mm diameter cylindrical probe. Note that initial force in *A* is the same as in *B*. Second traces indicate the firing rate of the unit having medium-sized spikes calculated for each 200 ms bin, third traces force and the fourth traces displacement. *C*, responses to stimuli applied with 1–10 mm diameter probes. The same constant force of 5 N was applied in all tests. *D*, responses to 1–9 N forces applied with a 6 mm diameter probe. Note that three units with different sizes and different thresholds can be distinguished in records *A*–*D*. Arrow in the uppermost record indicates onset of discharges of the smallest unit. All records were taken from flexor digitorium brevis in the same cat.

The stimulus–response relationship of the reflex was examined in single motor units in IO and FDB. For this analysis a servo-controlled actuator was used which could generate either constant force or constant displacement. In Fig. 2*A* and *B* the central pad was pressed with a disc probe (6 mm diameter) at a constant displacement (*A*) and at a constant force (*B*), respectively. It is shown that reflex discharges of the motor units (FDB) better reflected force stimuli rather than displacement stimuli. This was a consistent finding. In the following measurements, therefore, constant force stimuli were used.

Figure 2*C* shows firing of four to five motor units evoked by applying a constant force (5 N) to the central pad with probes of different diameter (1–10 mm). The reflex was progressively stronger when the diameter of the probe was smaller. This showed that the reflex originated from receptors which were effectively activated by localized stimuli causing sharp indentation of the pad skin.

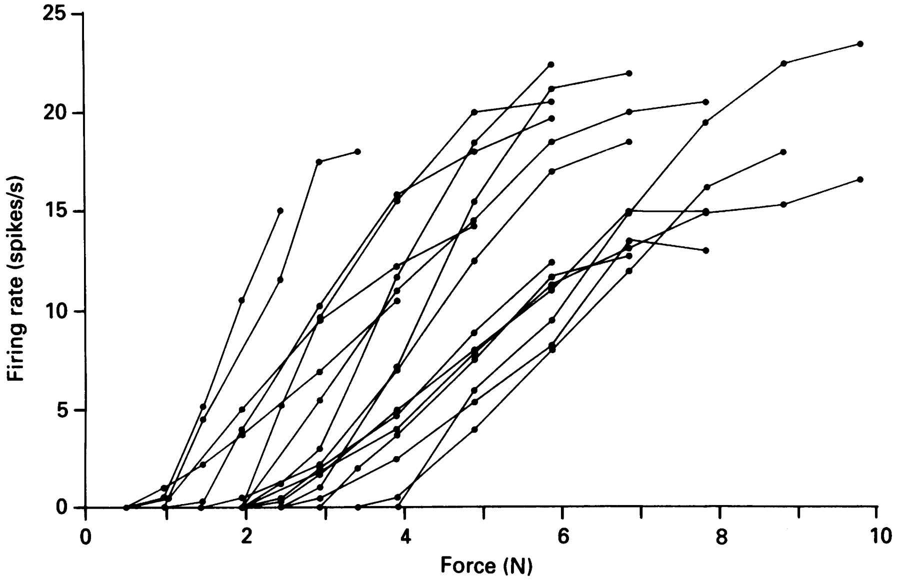

Fig. 3. Stimulus–response relationships of seventeen interosseus (IO) motor units. For each unit firing rates during the initial 2 s of constant force stimuli (ordinate) are plotted against the forces applied to the central pad (abscissa). Each data point represents the mean of four to six trials. Measurements were made for the stimulus range in which a particular unit was distinguished from the others. Constant force stimuli with 1 s rise times were applied to the central part of the pad with a 3 mm diameter probe. All units were recorded in the same animal.

Figure 2*D* shows recruitment of three distinguishable FDB motor units in response to progressively increased (from above downward) force stimuli with a 6 mm probe. The small motor unit (arrow) had a threshold below 1 N, the medium unit between 1 and 2 N, and the largest unit began to respond at 5 N. The small unit discharged tonically to all stimuli. Discharges of the two larger units showed adaptation at weaker stimuli, but became more sustained as the stimulus increased.

The relationship between the stimulus strength (force) and the firing frequency of a motor unit during the initial 2 s of the constant pressure period was obtained from records like those in Fig. 2*D*. Figure 3 shows the relationships for seventeen IO motor units sampled in the same animal, where care was taken to keep the conditions of pad stimulation as constant as possible. Note that thresholds were variable with units ranging below 1–4 N, and that each motor unit continued to increase its firing rate over a wide range of stimulus strengths (up to 6 N). Many units not showing a planteau in Fig. 3 would have further increased their firing rates with stronger stimuli, but contamination by other recruited units prevented quantification. The range of increase in the firing rate varied from unit to unit, and there was some tendency that motor units with lower thresholds had steeper slopes with the maximum frequency reached at weaker stimuli, while units with higher thresholds continued to increase their discharge frequency against stronger stimuli, 8 N or higher. Similar results were obtained in another cat in which six motor units (three IO and three FDB) were analysed. Since the muscle consisted of a spectrum of motor units responding to pad stimuli with different thresholds and incremental ranges, this should allow the whole muscle to respond in a graded manner for a wide range of stimuli in the plantar cushion reflex.

Different reflex effects evoked from the medial and lateral parts of the central pad

Local pressure stimuli applied anywhere on the central pad elicited reflex discharges in FDB, LS and IO of all four toes. However, the intensity of reflex EMG discharges varied considerably, particularly in muscles of the most medial and the most lateral toes, depending on the sites of stimulation within the central pad. The strongest excitation was usually from the central lobe, in toe extensors of any digit. Stimulation of the medial lobe gave rise to stronger excitation in muscles of the most lateral toe and weaker excitation in the most medial toe, while the relation was reversed when the lateral lobe was stimulated. Figure 4*A*–*C* illustrates responses of II-IO and V-IO to local stimuli applied to the three different lobes. Note a clear asymmetry in the magnitude and duration of responses between the two muscles (*B* and *C*). Similar mediolateral differences were observed in FDB and LS as well.

The asymmetrical effects from the medial and lateral parts of the central pad on extensors of different toes may not have been due entirely to a difference in strength of an excitatory effect. Some inhibitory effects, though weak, could occasionally be demonstrated when medial or lateral lobe stimulation was combined with stimulation of the central lobe. As shown in the upper records of Fig. 4*D* and *E*, for example, the EMG responses of II-IO evoked from the central lobe were slightly increased by simultaneous stimulation of the lateral lobe, but were reduced by stimulation of the medial lobe. Local mechanical factors would have had little influence, since additional stimuli caused differential effects on II-IO and V-IO. Hence the asymmetry of responses between the medial and lateral toe muscles, as in Fig. 4*B* and *C*, may have been partly due to concomitant inhibition. The inhibition from the lateral or the medial lobe was generally weak and not always present. For example it is not evident in the EMG records of V-IO in Fig. 4*D* and *E*, lower records. It seems important, however, that when the inhibitory effect was obtained, it was either from the medial lobe to extensors of the most medial toe, or from the lateral lobe to extensors of the most lateral toe.

Reflex actions from the toe pads

Excitatory effects

Reflex actions evoked by mechanical stimulation of the toe pads were quite different from those evoked from the central pad. Pressure stimuli applied to one of the toe pads usually did not cause any large movements of the toes nor of other proximal joints in agreement with Engberg (1964). In some animals, however, a small movement of the most medial or the most lateral toe was observed during stimulation of a toe pad. Though the reflex movement was generally very small and often difficult to detect, EMG recording indicated that it was due to reflex contraction of the toe extensors of the planta.

EMG recording consistently revealed that stimulation of the toe pads evoked reflex activities in extensors of the most medial and the most lateral toes, less frequently in the latter, and usually not in IO of the two middle toes. Characteristically, the receptive field of the reflex was different for the medial and the lateral toe extensors. Figure 5*A–D* illustrates examples of EMG responses recorded simultaneously from II-IO and V-IO during mechanical stimulation of individual toe pads (IIP, IIIP, IVP, VP). Note that II-IO was activated from the two lateral toes, VP and IVP (*D*, *C*), whereas V-IO was excited from the medial toes, IIP and IIIP (*A*, *B*). In both muscles the strongest excitation was evoked from the toe pad of the most distant digit and the activation from the next distant toe was usually much weaker, as in Fig. 5. EMG discharges of II-IO or of V-IO were never evoked from the toe pad of the same or the neighbouring digit (Fig. 5*A–D*) in any preparation. Similarly, the medial and the lateral part of FDB and LS muscles could be activated

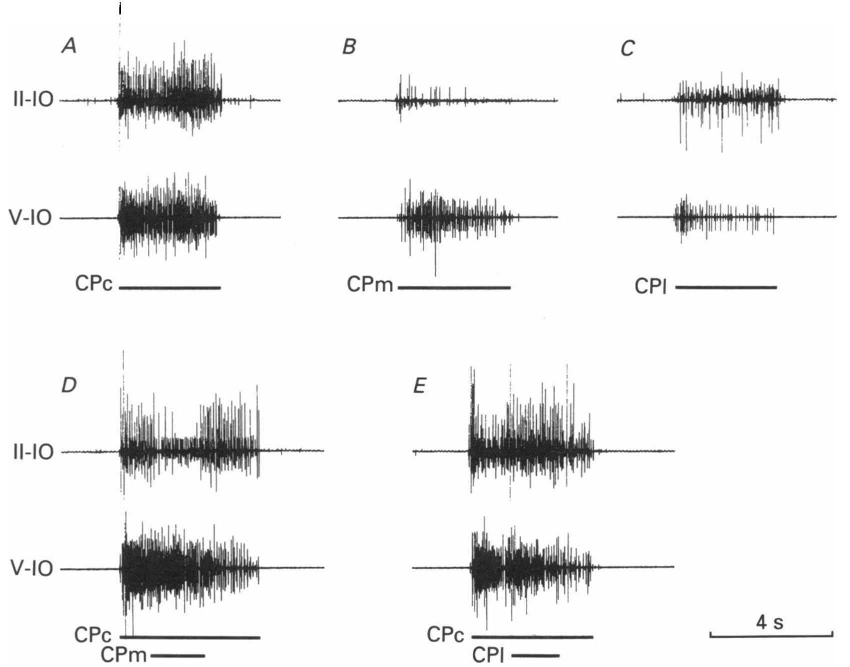

Fig. 4. Comparison of reflex effects from the medial and the lateral parts of the central pad. Each pair of traces indicates compound EMG responses recorded simultaneously from interossei of the second (II-IO, upper) and the fifth (V-IO, lower) digit. *A–C*, responses during stimulation of the central (CPc; *A*), medial (CPm; *B*) and lateral lobe (CPl; *C*) of the central pad. Pressure stimuli of approximately the same intensity were applied manually with blunt forceps. A clear asymmetry of responses in two muscles can be seen in *B* and *C*. *D* and *E*, effects of combined stimulations of different lobes. Stimulation of the medial (CPm; *D*) or lateral lobe (CPl; *E*) was given during stimulation of the central lobe (CPc). Note decreased (*D*) and increased (*E*) EMG activity in II-IO during the added stimuli.

from pads of the lateral and the medial toes, respectively, though the spatial selectivity was less evident in LS. In all three muscle groups, the maximum excitation obtained by toe pad stimulation was much weaker than that evoked by stimulation of the central pad (compare Fig. 5*A–D* with Fig. 5*E*).

Occasionally, TA showed a weak reflex activity in response to stimulation of the medial toe pad.

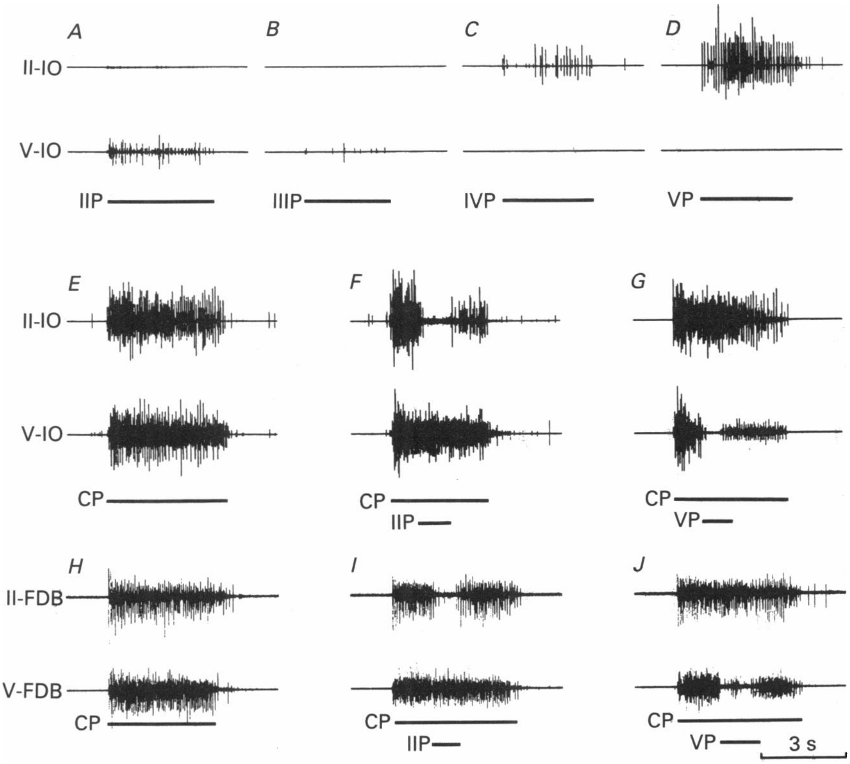

Fig. 5. Reflex effects from the toe pads. Compound EMG activity recorded simultaneously from II-IO and V-IO (*A–G*) and from II-FDB and V-FDB (*H–J*). *A–G* were recorded in the same cat. *A–D*, responses to stimulation of individual toe pads (IIP–VP). Both II-IO and V-IO are excited only from distant toe pads. *E–G*, effects of toe pad stimulation on central pad-induced activity. Moderate pressure stimulation of the second (IIP; *F*) and the fifth (VP; *G*) toe pad caused clear suppression of EMG activities evoked by stimulation of the central pad (CP) in the IO of the same toe. *H–J*, inhibitory effects from the toe pads on EMG activities of FDB. Stimuli are the same as in *E–G*.

Inhibitory effect: suppression of the central pad-evoked reflex

An inhibitory effect of pressure stimulation of toe pad was demonstrated as suppression of sustained EMG activity evoked by stimulation of the central pad. This is illustrated in Fig. 5, where the central pad-evoked EMG activity of II-IO is markedly depressed during stimulation of the second toe pad (Fig. 5*F*) and that of V-IO is inhibited by stimulation of the fifth toe pad (Fig. 5*G*). The suppression continued during application of pressure to the toe pad and remained virtually unchanged even with stimuli maintained for more than 5 s (not illustrated). This suggests that the inhibitory action also originated from slowly adapting mechanoreceptors. It was often noted that the reflex activity due to a maintained stimulus to the central pad did not fully recover after the cessation of toe pad stimulation (Fig. 5*F* and *G*), as compared with responses to central pad stimulation alone (Fig. 5*E*).

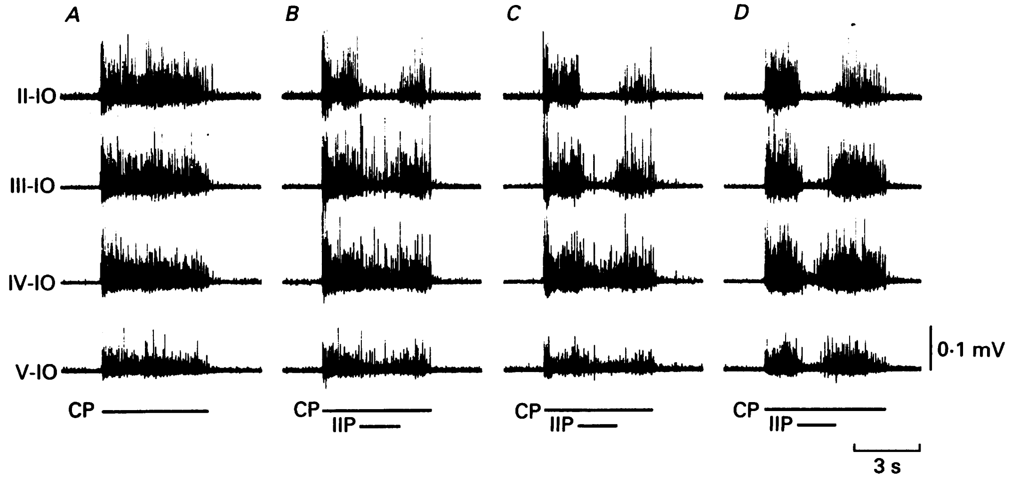

Fig. 6. Suppression of central pad-induced reflex activities of individual IO nerves by combined stimulation of the second toe pad. Each set of traces represents simultaneous records of discharges in the nerves innervating IO of individual toes (top to bottom, II-IO to V-IO). *A*, control responses during stimulation of the central pad (CP) alone. *B–D*, responses during combined stimulation of the central pad and the second toe pad (IIP). The second toe pad was stimulated with increasing intensities from *B* to *D*, while the central pad stimulus was kept at approximately the same as in *A*.

It was a consistent finding, as shown in Fig. 5*F* and *G*, that inhibition of II-IO was evoked from the second toe pad but not from the fifth toe pad, and V-IO was inhibited from the fifth toe pad but not from the second toe pad. A similar difference was consistently observed between II-FDB and V-FDB, and also between III-LS and V-LS (the second toe lacks LS). An example with FDB is shown in Fig. 5*H–J*. Thus, the IO and FDB of the second and the fifth toe were inhibited potently from the pad of their own toe and very little from the most distant toe.

The spatial pattern of inhibition produced by stimulation of each toe pad was studied in more detail by simultaneously recording from the isolated nerves innervating IO of individual toes in four cats. Compared with recording EMG, recording from the dissected muscle nerve has the advantage of evaluating mass activities of all the motor fibres to a particular toe without contamination of motor activities in other toes. The nerve recordings probably included discharges of γ-motor fibres, but spike amplitudes of γ-fibres would be much smaller than those of α-motor fibres (Sears, 1964), and discharges in Figs 6 and 7 are most likely of mainly α-fibres. Figure 6 exemplifies the suppression of central pad-evoked discharges by stimulation of the second toe pad at different intensities. In agreement with the EMG observations described above, all the four nerves innervating IO of individual toes exhibited intense reflex discharges in response to a maintained pressure applied to the central pad (Fig. 6*A*). In Fig. 6*B–D*, pressure stimulation of the second toe pad was added in the middle of central pad stimulation. The stimulus to the toe pad was increased in three steps from *B* to *D*, while the strength of central pad stimulation was kept constant, as in *A*. When the stimulus to the second toe pad was weak, suppression of the central pad-evoked discharge was seen almost exclusively in II-IO (*B*). With increase of stimulus intensity, suppression of discharge became clear also in IO of the neighbouring toe (*C*) and with further increases in those of distant toes (*D*). Note that in *D* the inhibition was most potent in II-IO and weaker and shorter lasting in more distant toes.

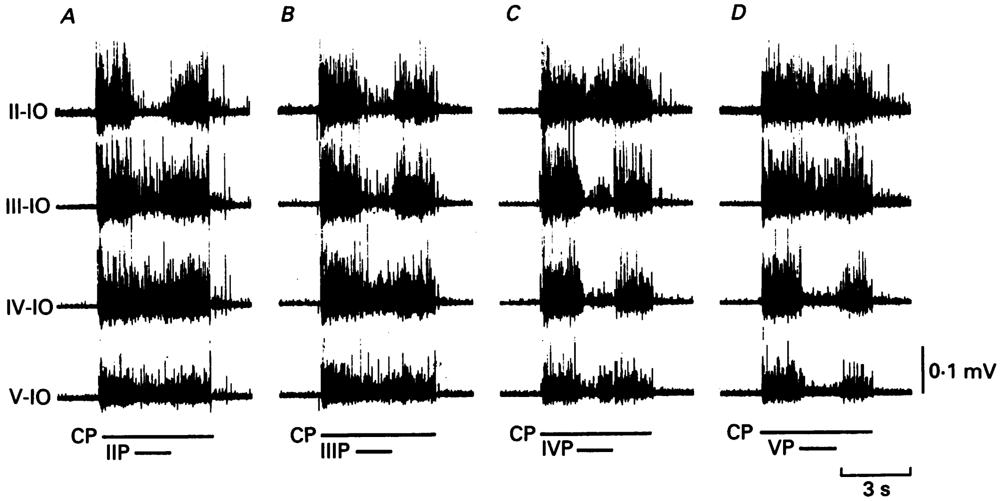

Fig. 7. Spatial patterns of inhibition evoked from individual toe pads. *A–D*, simultaneous records of discharges in the nerves of II-IO to V-IO. In each set of records, each toe pad (IIP–VP) was stimulated with pressure during stimulation of the central pad (CP).

Figure 7 compares the spatial patterns of inhibition evoked by stimulation of different toe pads with approximately the same pressure. To reveal differences in the spatial pattern of inhibition from different toe pads, weak stimuli producing well-localized inhibition (Fig. 6) were employed. In each of II-V IO nerves suppression of discharges was most prominent when the pad of its own toe was stimulated. As the stimulation became distant, the inhibition decreased and became less obvious.

While stimulation of a toe pad invariably caused suppression of central pad-evoked discharges in IO of the same and neighbouring digits, effects on those of the farthest toes were variable among preparations. Weak suppression was observed in some animals (Figs 6 and 7), and no effects or excitation in others (Fig. 5*G*). In the latter case a toe pad stimulus alone usually caused some excitation (Fig. 5*D*). It was occasionally observed in these preparations that some motor units increased their discharge rates while others in the same muscle ceased to fire. These observations indicated that effects from the toe pad on extensors of distant toes are a mixture of both inhibition and excitation, and the predominance of either inhibition or excitation could vary among motor units.

The reflex from the toe pads described above was distinct from the general flexion reflex in pattern. Mechanical thresholds of the toe pad reflex were approximately the same as those of the central pad-evoked reflex, and much lower than those producing withdrawal of the whole hindlimb. Light pressure could often almost completely suppress the central pad-evoked reflex discharges in muscles of the stimulated toe, and on increasing the stimulus the inhibition attained its maximum well before the stimulus caused, though occasionally, a flexion movement in the proximal joints.

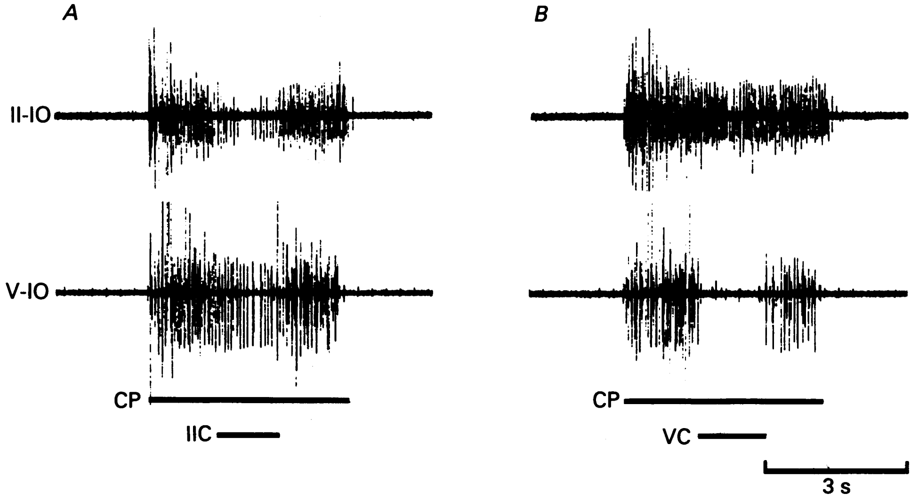

Fig. 8. Suppression of central pad-induced EMG activity by stimulation of the claw bases. *A* and *B*, simultaneous records of EMG activity of II-IO and V-IO during stimulation of the central pad (CP) combined with pressure stimulation of the base of the second (IIC; *A*) and the fifth claw (VC; *B*).

Reflex actions from other skin areas of the foot

No obvious excitatory reflex was evoked by moderate pressure stimuli to any skin areas other than the pads, but inhibition of central pad-evoked discharges of toe extensor muscles was obtained by stimulating the skin at the claw bases and also its contiguity on the dorsum of the toe. The spatial pattern of the inhibition was similar, though somewhat less distinct, to that evoked from the toe pad, as shown in Fig. 8*A* and *B* for effects from the claw bases. The inhibitory effects from these regions were usually weaker than those from the toe pads.

The effective stimulus to the claw region was pressing (nipping) the skin at the claw bases from both sides, or twisting or bending the claw so as to deform the region of claw base. Light touch of the skin at the claw bases (Gordon & Jukes, 1964; Brown, Fyffe, Rose & Snow, 1981) was ineffective. Since the inhibitory effect lasted as long as the stimulus was applied (Fig. 8*B*), slowly adapting mechanoreceptors must have contributed. Inhibition from the toe dorsum was also produced by pressure and adapted only slowly. While the area is hairy, stimulation of hairs alone was without effect.

DISCUSSION

Organization of reflexes from the foot skin

Spatial patterns

The main outcome of the present study is the disclosure of highly specialized reflex patterns onto foot muscles evoked from the skin of the sole, particularly the toe pads. A striking feature of the reflexes from the toe skin is that they act differentially on extensors of individual digits and the spatial pattern of actions is specifically dependent on the skin locus stimulated. Stimulation of the fifth toe pad, for example, produces strongest inhibition of toe extensors in the fifth digit and weaker and weaker inhibition in the fourth and third digits, and the effect may be changed to excitation in the second digit. When the second toe pad is stimulated, a reversed pattern is obtained. Thus, the basic pattern of the reflex is dominant inhibition centred on the stimulated digit with an occasional mixed excitation in the most distant digit.

The reflex actions evoked from the central pad, the plantar cushion reflex, are distinct from those from the toe pads. In agreement with previous findings (Engberg, 1964; Egger & Wall, 1971), a dominant effect elicited from the central pad is excitatory and appears in extensors of all the digits. Nevertheless, the present results indicate that the degree of excitation in individual digits also varies depending on the stimulation site: stimulation of the medial or the lateral part of the central pad causes stronger excitation in toes distant from the stimulus. Our results also suggest that the weaker excitation in closer toes is due to inhibition. The mediolateral difference is qualitatively similar between reflexes from the central pad and from the peripheral pads, though excitation predominates in the former. Sherrington's (1910) observation in the spinal monkey that excitation of the outer edge of the planta causes some eversion of the foot and that of the inner edge some inversion, along with ankle flexion, may have some relevance to the mediolateral differences in reflexes of the cat foot found in the present study.

The reflexes evoked from the toe pads as well as those from the central pad were consistently observed in preparations anaesthetized with routine doses of sodium pentobarbitone (40 mg kg^{-1}). Their patterns were not changed by spinalization at the lowest thoracic level. These specialized reflexes are, therefore, quite potent and their pathways are likely to be concretely built in the spinal cord. The slight augmentation of the reflexes after spinalization was probably due to removal of tonic inhibition from higher levels (Eccles & Lundberg, 1959*b*; Holmqvist & Lundberg, 1961).

The study of EMGs and nerve discharges does not allow us to specify whether the reflex inhibition was due to postsynaptic inhibition of motoneurones or to other mechanisms such as disfacilitation (inhibition of excitatory interneurones) or presynaptic inhibition. Another study has revealed, however, that postsynaptic inhibition of motoneurones does play an important role in the localized inhibitory reflex evoked from the toe skin (Hongo *et al.* 1985).

Receptor origin

The localized reflexes evoked from the toe pad were typically of tonic nature. This was true for both excitatory (Fig. 5) and inhibitory (Figs 5–7) effects. Hence the reflexes originated from slowly adapting mechanoreceptors, as does the reflex from the central pad (Engberg, 1964; Egger & Wall, 1971). The time course and stimulus–response relations of the central pad-evoked reflex (Fig. 3) were comparable with those of pressure receptors or slowly adapting mechanoreceptors previously reported (Jänig, Schmidt & Zimmermann, 1968; Ferrington, 1985). The pressures applied to the toe pads were not quantitatively measured for technical reasons. However, thresholds of mechanical stimulation for eliciting the excitatory and inhibitory reflexes were low and similar to those for the reflex from the central pad (assessed subjectively by pressing or pinching the toe pads with blunt forceps). It is, therefore, very likely that the receptors for both reflexes are of the same type. Previous physiological and morphological findings show that slowly adapting mechanoreceptors in the pad skin are mainly type I in the cat (Jänig *et al.* 1968; Jänig, 1971*a*, *b*; Brown, Rose & Snow, 1978; Ferrington, 1985), whereas in many other species there are both type I and type II slowly adapting receptors (Johansson, 1978; Pubols & Pubols, 1983; Rasmussen & Turnbull, 1986), as in the hairy skin (Iggo, 1966; Burgess, Petit & Warren, 1968; Iggo & Muir, 1969; see also Burgess & Perl, 1973).

Weaker but essentially similar patterns of reflex as those from the toe pads were evoked from the neighbouring skin, the base of a claw and its contiguous hairy skin of the toe dorsum. Egger & Wall (1971) reported that squeezing the skin between the toes inhibited the central pad-evoked movement of the toes, and this corresponds with present observations. Reflexes from these extra-pad regions also lasted during prolonged stimuli, showing that slowly adapting receptors contribute to these reflexes as well (Fig. 8). It is likely that these reflexes are akin to the toe pad-evoked reflexes and should be considered together, since both are caused by tonic deformation of the skin of single toes and show similar patterns. Afferent fibres from type II slowly adapting mechanoreceptors at the claw base (Gordon & Jukes, 1964; Brown, Gordon & Kay, 1974; Brown *et al.* 1981) probably contributed to the reflex, though involvement of other afferents cannot be excluded. If so, this would be an indication of a combined contribution of both type I and type II slowly adapting receptors to the same reflex, though the two kinds of afferent fibre have different patterns of projection in the grey matter. Type I afferents terminate in laminae III, IV and the dorsal part of lamina V (Brown *et al.* 1978) and type II claw afferents in laminae III-VI (Brown *et al.* 1981). The type of receptor responsible for the localized reflex evoked from the hairy skin of the digit remains to be clarified.

Functional roles of the reflexes from the foot glabrous skin

The reflex discharges evoked from the central pad in toe extensors were shown to appear in a graded manner when pressure stimuli of increasing strength were applied (Fig 1*C*). Analysis of motor unit responses revealed that the graded nature of the reflex was due to two mechanisms, i.e. (1) a progressive increase in firing frequency of each unit and (2) recruitment of additional motor units with higher thresholds, in response to stronger stimuli (Fig. 3). Because the firing frequency of individual units increased with increasing stimulus strength (up to 6 N with a 6 mm probe) and because of large differences in recruitment threshold (0·5–4 N), the reflex response of the whole muscle could be graded over a wide range of stimulus strengths. The inhibitory effects from the toe skin were also graded over a wide range (Fig. 6). By changing the intensities of stimuli applied to the central pad and to the toe pad, activity of toe extensors could be varied from strong plantar flexion of the digit to complete relaxation. The graded nature of both excitatory and inhibitory reflexes would allow fine control of tonic activities of toe extensor muscles against a variety of pressure stimuli to the foot pads. It is important to note that the range of forces used approximately corresponds to the body weight to be supported by a limb.

Since the reflexes from the central pad and from the toe pads are assumed to originate mainly from slowly adapting mechanoreceptors of the same category, and since both the reflexes participate mainly in the control of toe movements, it is reasonable to consider their function in combination. Suppose that the animal is standing on flat ground with all the cental pad and the peripheral pads in contact with the ground and supporting the body weight. If the pressure to the central pad is increased for some reason, e.g. on a downhill gradient, the resultant plantar flexion of the digits would increase the pressure on the toe pads and decrease that on the central pad. If on the other hand the peripheral pads become overloaded, the toe pad-evoked inhibition of the toe extensors would cause the reverse effect. Thus, in both cases, the reflexes would function to minimize the unbalanced loads between the central pad and peripheral pads (anteroposterior adjustment). A mediolateral imbalance of loads would also be adjusted reflexly. If, for example, the lateral part of the foot is overloaded, inhibition of the extensors of the lateral toe and excitation of the medial toe caused by afferents from the lateral toe and, though weak, from the lateral lobe of the central pad would improve the mediolateral unbalance by decreasing the supporting force of the lateral toe and increasing that of the medial toe. Moreover, when the animal is standing on rugged ground, differential reflex actions from the toes would be helpful for adjusting the position of individual digits to adapt them properly to the ground. These interpretations are extensions of Engberg's (1964) proposal that the reflex from the central pad may serve to stabilize the foot. The functional coupling between the reflexes from the central pad and those from the toe pads may play an important role in the control of toe movements.

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