The Role of Cutaneous Afferents from the Distal Hindlimb in the Regulation of the Step Cycle of Thalamic Cats

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Summary. The pad and the plantar surface of the foot were stimulated electrically in thalamic cats. Weak stimulation evoked an extensor reflex in the animal at rest. The same stimuli in a spontaneously walking animal applied during the stance phase produced an increase both in amplitude and duration of the ongoing extensor activity. When given during the swing phase, the stimuli either prolonged the ongoing flexor activity and/or shortened the following extensor burst. These changes in flexor and extensor burst duration were reflected in changes in the step cycle duration.

Similar results were seen with direct stimulation of the sural nerve. For the latter experiments the ipsilateral hindlimb was fixed and denervated except for the ankle extensors and flexors, which showed rhythmic contractions correlated normally with the walking movements of the three remaining limbs. At rest, threshold stimulation of the sural nerve evoked a reflex contraction in the triceps surae of the fixed leg. The same stimuli applied during the contraction phase of the fixed triceps surae during walking resulted in a larger and longer extensor contraction and a delay of the following flexion. Stimulation during the relaxation phase of the fixed triceps surae reduced the duration of the following contraction phase. The findings are discussed in relation to the possible role of cutaneous input during locomotion.

Key words: Cutaneous afferents — Locomotion — Thalamic cats — Sural nerve.

Introduction

Since cutaneous stimulation of the distal limb was found to produce various extensor reflexes in animals at rest (extensor thrust: Sherrington, 1906; positive supporting reaction: Magnus, 1926; "stützreaktion": Pritchard, 1926; Schoen, 1926; toe extensor reflex: Engberg, 1964), it was suggested very early that reflexes of this type might serve to reinforce the extension during the locomotory stance phase (Sherrington, 1906; Philippson, 1905). However, this hypothesis failed to be proven, since denervation or anaesthesia of the foot yielded very small deficits in the walking behaviour of cats (Sherrington, 1910; Engberg, 1964). Sherrington concluded that cutaneous reflexes may contribute but are not indispensable to locomotion.

Recently Grillner (1975) has pointed out that the negative evidence could be attributed to inadequate testing conditions and it is possible that deficits would be revealed if cats were allowed to walk on unpredictable surfaces. Also, it is conceivable that different afferent systems serve the same purpose and the proprioceptors of the limb may take over the role normally played jointly by exteroreceptors and proprioceptors. Therefore, selective activation of cutaneous receptors during locomotion may provide more information than can be obtained from denervation experiments. In a previous study by Forssberg *et al.* (1975) it was shown that stimulation of the dorsum of the foot during walking results in a phase dependent reflex reversal. It was found that stimulation during the swing phase enhanced the flexion of the stimulated hindlimb while stimulation during the stance phase evoked a shorter but more pronounced extension. No data are available on the stimulation of other skin areas during locomotion. In the present study, the role of exteroceptive input from the pad and the plantar surface of the foot was examined by electrically stimulating the skin or the skin nerves of the distal hindlimb during spontaneous locomotion of thalamic cats. When put on a treadmill, this preparation is able to walk with a speed that is appropriate for the speed of the belt. The precise adjustment of the step cycle duration to the belt speed is achieved by varying the duration of the stance phase, the swing phase being of relatively constant duration (Orlovskii and Shik, 1965). Variations in duration of the stance phase are presumably brought about by phasic afferent input during walking. The extent to which muscle, joint and skin receptors play a role in this process is unknown but it is possible that cutaneous afferents from the pad and the foot are involved since these afferents provide the animal with valuable information about the loading conditions of the limb during locomotion (Grillner, 1973). The present study was undertaken mainly to investigate the possible role of cutaneous input in the regulation of the step cycle.

Methods

Experiments were done on 16 cats weighing 2—4.5 kg. Until decerebration the animals were kept anaesthetized with Halothane. Throughout the entire experiment the blood pressure was continuously monitored through an intra-arterial cannula and a 6% dextrose solution was given intravenously if the blood pressure fell below 100 mm Hg. Two groups of cats were prepared. One group was used for the experiments with electrical stimulation of the skin. Two silver plate electrodes of 6 mm diameter were attached to the shaved skin of the central plantar surface of the foot (interelectrode distance 1—2 cm) or to the central and peripheral lobes of the hindlimb pad. Another group of cats was prepared for direct stimulation of cutaneous nerves. In these animals the left hindlimb was completely denervated except for the nerves to the ankle extensors and flexors. The left sural nerve was freed from surrounding tissue and cut at the level of the triceps.

All animals were then fixed in a stereotaxic frame mounted over a motor driven treadmill. The denervated group of cats, used for sural nerve stimulation, had their left hindlimbs rigidly fixed to a frame while the three other limbs were allowed to move freely. A paraffin bath was made at the knee of the fixed limb and the sural nerve was mounted on bipolar stimulating electrodes. In some experiments the left Achilles tendon was attached to a force transducer. The group of cats prepared for skin stimulation had all four limbs intact.

Two copper wires, insulated except for the tip, were inserted in the triceps surae bilaterally in all animals to record the electromyographic activity (EMG) differentially. The electrode
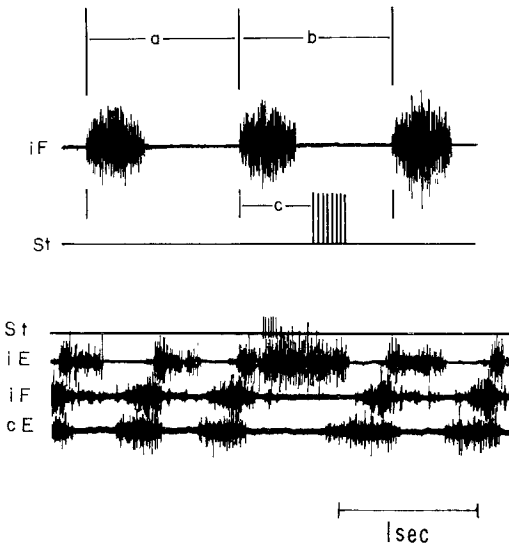
Fig. 1. (Top) Parameters used to evaluate the effect of tetanic stimulation on step cycle duration. Upper trace: rhythmic EMG bursts of ipsilateral pretibial flexors (iF). Lower trace: stimulus (st). (a) Duration of step cycle preceding the step cycle with stimulation. (b) Duration of step cycle during which stimulation was started. (c) Time between onset of step cycle and onset of stimulus train. (Bottom) The increase in amplitude and duration of extensor activity following stimulation of the central plantar surface of the foot during the stance phase of a thalamic cat walking on a treadmill. A short train of six weak electrical shocks (St., 1 msec, 60 Hz) given immediately after the first extension phase evokes a long and intense discharge in the ipsilateral ankle extensors (iE). The prolonged extension is associated with a delay in the onset of the next EMG burst of the ipsilateral pretibial flexors (iF) and the contralateral ankle extensors (cE)

tips were placed within a distance of less than 1 cm from each other in order to sample the same muscle (medial or lateral gastrocnemius, soleus) but no systematic choice of one of these three muscles was made over all the experiments. In most cases the EMG of the pretibial flexors, tibialis anterior and extensor digitorum longus, was also monitored.

All cats were decerebrated with a cut in front of the colliculi and the mammillary body, leaving the optic chiasm intact (Grillner and Shik, 1973). The decerebration was performed with the aid of a stereotaxically guided spatula. Despite only very minor changes in the exact level of brain stem transection, there was some variability in the duration and quality of locomotion, related to the general condition of the animal. For this study only the best periods of spontaneous locomotion were chosen. During these periods, the walking was almost indistinguishable from the normal cat: regular, stable walking pattern, no sham rage, active extension, etc. Satisfactory walking was obtained in such "thalamic preparations" for periods ranging from 30 min to 5 hours. The speed of the treadmill belt was kept around 2.7 km/hour. In the partially denervated cats normal stepping of the three intact limbs was observed synchronously with rhythmic contractions of the isolated left ankle extensors. These contractions had an amplitude, duration and timing which would have been expected from these muscles if the limb were allowed to move freely.

To stimulate the skin and the sural nerve, 50—600 msec trains of rectangular pulses (1 msec duration) were delivered at regular intervals of 3—5 sec through an isolation unit. The interval was chosen such that there was no synchronization of stepping rate and rate of

stimulation. The frequency of stimulation within a given train was either 60 or 80 Hz. The stimuli, EMG and isolated triceps surae force were displayed on a four-channel cathode-ray oscilloscope and recorded on magnetic tape.

Data Analysis

All data were filmed with speeds ranging from 2.5—10 cm/sec. To study the effects of cutaneous stimulation on the rate of stepping, measurements were made of the step cycle during which the stimuli were given and these measurements were compared with measurements of preceding and following step cycles (Fig. 1, top). The step cycle duration was defined as the period between the onsets of subsequent EMG bursts in the ipsilateral pretibial flexors (a and b in Fig. 1, top).

In a few cases where no satisfactory ipsilateral flexor EMG could be obtained because of pick-up of electrical activity from extensors, the end of the ipsilateral extensor burst was taken as the start of the step cycle. The difference in duration between the cycle during which stimulation occurred and the preceding cycle (b—a) was plotted against the time between cycle onset and onset of stimulation (c in Fig. 1, top). To normalize the data, both the cycle time difference (b—a) and the time to onset of stimulation (c) were expressed as a % of the preceding cycle.

Most data were obtained by direct measurement from film records but in order to improve accuracy some data were analyzed by computer (PDP 8). For this purpose the EMG traces were integrated and a computer program, written by R.B. Stein, allowed automatic computation of the time between onset and offset of EMG bursts.

Results

1. Stimulation of the Plantar Surface of the Foot and the Pad

a) Plantar Surface of the Foot

Weak electrical stimulation of the plantar surface of the foot of a thalamic cat under *resting* conditions evoked a small reflex contraction of the ipsilateral triceps. Stimuli which were 10—20 times stronger elicited a reflex flexion of the whole limb (flexor reflex). These two classes of stimuli, one producing an extensor, the other a flexor reflex, will from now on be classified as "weak" and "strong". The transition from an extensor reflex to a flexor reflex with increasing stimulus intensities has been described by Sherrington (1904, 1911).

The weak stimuli, a 300 msec train of 1 msec pulses at 60 Hz, were then applied at regular intervals during the periods of spontaneous walking. Since no attempt was made to synchronize all stimulus trains with a particular phase of the step cycle, application of the stimuli was essentially at random within the step cycle.

When the weak stimuli fell within the stance phase of the ipsilateral hindlimb a marked effect on the ipsilateral extensor activity was observed (Fig. 1, bottom). Both amplitude and duration of the ipsilateral triceps EMG burst were increased. There was also a corresponding delay in the onset of the subsequent activity in the ipsilateral flexors and the contralateral extensors. Taken together, these changes produced a bilateral prolongation of the step cycle, defined as the sum of a flexor and an extensor EMG burst. The situation was quite different when weak stimuli were applied during the swing phase. This is illustrated in Fig. 2 obtained from another experiment. Figure 2A shows how stimuli given at the beginning of the
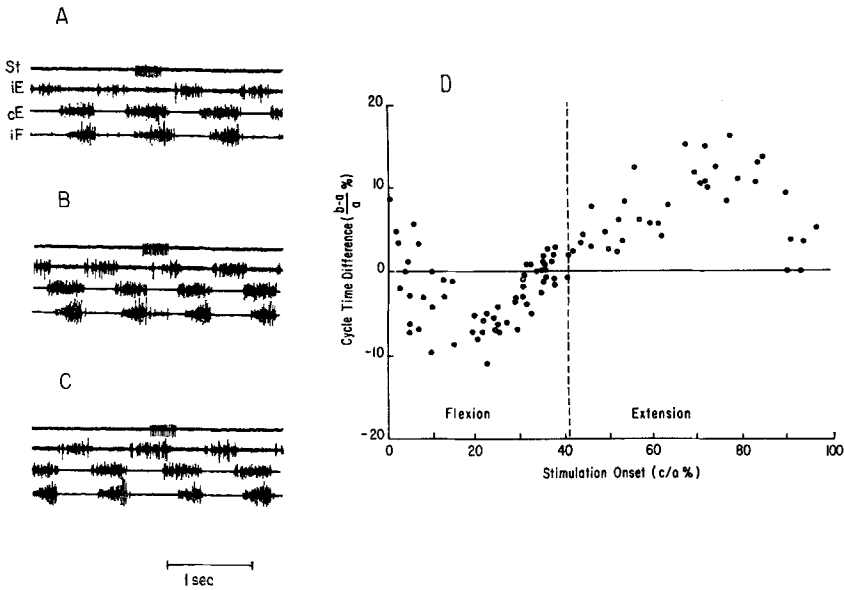
Fig. 2. Step cycle changes evoked by electrical stimulation of the central plantar foot at different moments of the ipsilateral step cycles. A prolongation of the cycle is evoked by a prolongation of either the flexor burst (A) or the extensor burst (C) depending on the time of stimulus onset. In B, the shortening of the extensor burst results in a shortening of the step cycle. These phase dependent effects are summarized in D. Notice the prolongation of the step cycles when the stimulus train starts either early in the phase of flexor activity (cfr A and extreme left of D) or during the period of extensor activity (cfr C and right side of D). Otherwise a shortening is seen. Stimuli: square pulses of 1 msec, 60 Hz, in 300 msec trains at 3—5 msec intervals

ipsilateral flexor activity prolonged the flexor EMG burst while having no appreciable effect on extensor activity. Thus the over-all effect is again a prolongation of the step cycle but this time it is the longer flexor burst which is responsible for the step cycle prolongation. In between is the situation with weak stimulation starting in the middle of the swing phase (Fig. 2B). The stimulus train, extending over the end of the flexor and the beginning of the extensor burst, caused a prolongation of the ipsilateral flexor activity while at the same time reducing the duration and the amplitude of the ipsilateral extensor burst. The shortening of the extensor activity caused a shortening of the step cycle. The three situations with stimulation at the beginning (Fig. 2A), middle (Fig. 2B) and end (Fig. 2C) of the step cycle are further described in Fig. 2D. The duration of the step cycle during which stimulation was started was compared to the duration of the just-preceding step cycle and this difference was plotted against the interval between the onset of the cycle and the onset of the stimulus train (see Methods). Thus data points lying above the horizontal zero axis indicate a prolongation of the step cycle while the lower points indicate a shortening. On the average, the step cycle just preceding the cycle with stimulation had a duration of 787 msec (S.D. = 23 msec or 2.9%). Flexor EMG activity accounted on the average for the first 41% of this time

(vertical dashed line in Fig. 2D). The effects on step cycle duration described for Fig. 2A, B and C are readily recognized in Fig. 2D. Step cycle prolongations are noted when stimulation starts in the stance phase and early swing phase. A pulse train given in the middle of the swing phase caused a shortening of the step cycle. Again, as for Fig. 1 (bottom), the lengthening of the ipsilateral step cycles was correlated with a lengthening of the contralateral cycles. In the stimulated limb there was a clear tendency for the prolonged or shortened step cycles to be followed respectively by a shorter or longer step cycle, indicating a return to the control rate of stepping.

b) Pad

Simular results were obtained when the pad was stimulated instead of the plantar surface of the foot. *At rest*, weak pulses (60 Hz) applied to the plantar cushion for a period of 400 msec evoked a toe extensor reflex (Philippson, 1905; Engberg, 1964). Slightly stronger stimuli evoked ankle extension, indicating a transition from the toe extensor reflex to the extensor thrust (Sherrington, 1910). Finally, very strong stimuli evoked a flexion of the ipsilateral hindlimb (flexor reflex; Sherrington, 1910).
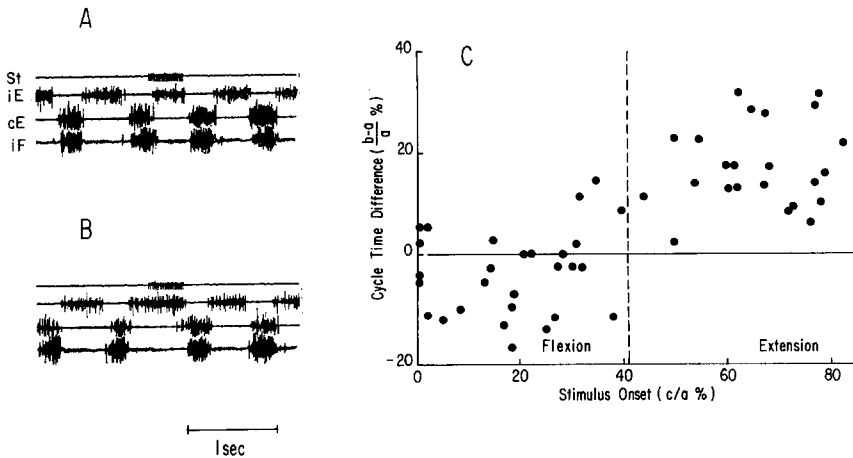

Fig. 3. Effect of electrical stimulation of the pad at different moments in the step cycle. (A) Pad stimulation starting during the flexor burst (*iF*) has an inhibitory effect on the amplitude and duration of the activity of the ipsilateral triceps surae (*iE*). The shortening of the step cycle is due to the short extensor burst while the flexor burst is unchanged. (B) Stimulation of the pad during the ipsilateral stance phase. The ipsilateral extensor activity is prolonged and the next flexor burst is delayed causing a prolongation of the step cycle. (C) The changes in step cycle duration observed in A and B are plotted for a large sample of consecutive step cycles. Abscissa and ordinate as in Fig. 2D. Stimulation starting in the period of flexor activity causes a shortening of the step cycle while stimuli applied during the extensor activity prolong the step cycle. Stimulus parameters are the same as for Fig. 2D but duration of pulse train is 400 msec

Weak stimuli were now applied during *walking*, producing much the same results as in the case of the plantar foot stimulation. Stimulation starting during the period of activity of the ipsilateral flexors resulted in a shortening of the step cycle of up to 20% (Fig. 3A, C), while stimulation starting during the activity in the ipsilateral extensors gave cycle prolongations of up to 30% (Fig. 3B, C). The larger scatter in Fig. 3C is probably linked to the more irregular walking during the period analyzed for Fig. 3C as compared to the period used for Fig. 2. In fact, the variability of the control cycles for Fig. 3C was much larger (S.D. = 51.7 msec or 7.4%, mean cycle duration = 702 msec).

2. Stimulation of the Sural Nerve

In the previous section it was assumed that mostly cutaneous receptors would be stimulated by the electrical shocks. However, the possibility that underlying muscle was also activated could not be excluded. Therefore, it was important to include experiments with direct stimulation of cutaneous nerves. For this purpose the sural nerve was dissected free in a hindlimb which was extensively denervated except for the ankle extensors and flexors (see Methods).

At rest, weak tetanic sural nerve stimulation evoked a reflex contraction of the ipsilateral isolated triceps surae with a delay of 30 msec (inset in Fig. 4). This is in
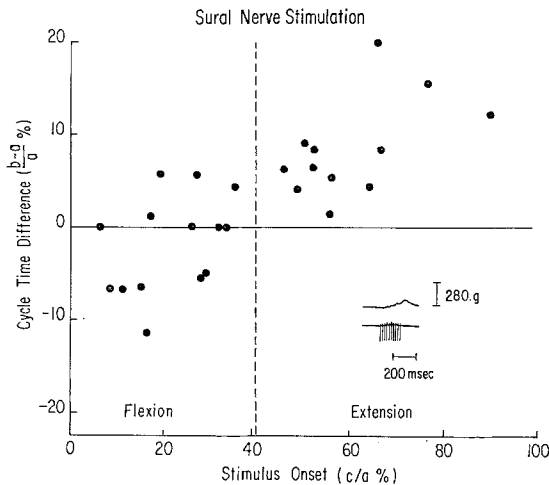

Fig. 4. Influence of weak tetanic sural nerve stimulation on the rhythmic contractions of ipsilateral ankle extensors and flexors during locomotion. Coordinates as in Fig. 3. The ipsilateral hindlimb being fixed, the "step cycle" duration is taken as the time between the onset of consecutive EMG bursts in the fixed pretibial flexors. Sural nerve stimulation starting during the contraction phase of the isolated triceps surae prolongs the triceps surae contraction and thus also the step cycle. Stimulation at an earlier time in the step cycle tends to shorten the step cycle. A 180 msec train of 1 msec pulses was used at 60 Hz. In the inset this same stimulus given to a resting animal is shown to produce a reflex contraction of the isolated triceps surae with a latency of 30 msec. An example of very pronounced step cycle prolongation falling completely beyond the scale of the ordinate of this graph is illustrated in Fig. 5B
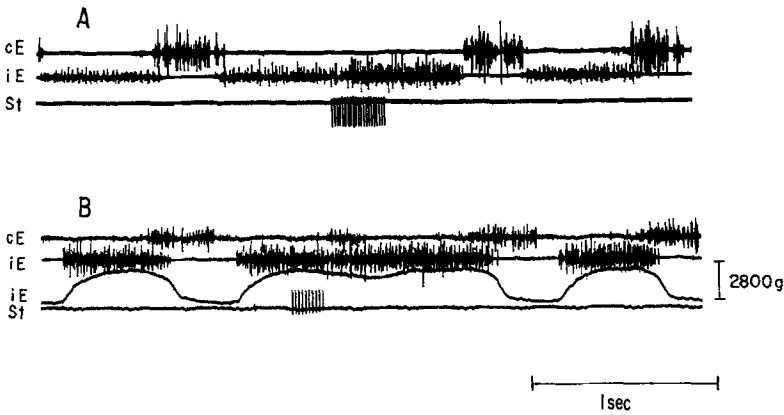
Fig. 5. Repetitive stimulation of the sural nerve at the end of the stance phase prevents the rhythmic relaxation of the ipsilateral triceps surae (iE). Concomitant with the prolongation of the ipsilateral extensor contraction there is a complete (A) or partial (B) inhibition of the contralateral extensor EMG (cE). For (A) a stimulus train of 280 msec (80 Hz) was used. In (B) 60 Hz stimulation was given for 150 msec. The stimuli shown in (A) and (B) evoked an extensor reflex in the resting animal. (A) and (B) are from different cats but (B) is from the same cat as in Fig. 4. Force calibration is for the third trace in (B), showing the force exerted by the ipsilateral triceps surae (iE)

agreement with previous work by Hagbarth and Naess (1950) who showed that there is a facilitation of the ankle extensors after 30 msec of repetitive stimulation of the sural nerve. To determine the type of afferent fibers involved in this extensor reflex, L7 dorsal root recordings were made in some animals. The afferent volley, evoked by threshold stimulation of the sural nerve, reached the dorsal root with a latency of 2.5—3 msec, indicating that fibers with a conduction velocity of 73—88 m/sec were activated. Such fibers are amongst the largest found in the sural nerve (Hunt and McIntyre, 1960; Whitehorn et al., 1974).

Trains of weak stimuli were then applied during the periods of walking (Fig. 4). When given during the swing phase, the stimuli tended to reduce the amplitude and duration of the next extensor burst, causing a slight reduction in cycle duration. The most striking effect, however, was seen when stimulation was delivered during the period of extensor activity. The pulse train both enhanced and prolonged the extensor activity and caused a prolongation of the cycle. Sometimes the prolongation was more marked than can be seen in Fig. 4, since several points fell completely beyond the scale of the ordinate of the graph. Such examples are illustrated in Fig. 5. A stimulus train given near the end of the stance phase prolonged the step cycle for almost 100%. This appeared to be due to deletion of one period of relaxation. In all cases where an ipsilateral flexor EMG was obtained it was noted that the flexor activity was completely suppressed during the prolonged step cycles. Moreover, omission of extensor relaxation occurred simultaneously with a complete (Fig. 5A) or partial (Fig. 5B) disappearance of the contralateral extensor activity.

Discussion

Electrically stimulating the pad or the plantar surface of the foot of a resting thalamic cat evokes a reflex contraction of the ipsilateral ankle extensors, while the same stimuli applied during the hindlimb stance phase of a walking cat prolong the ongoing stance by extending the period of extensor activity and delaying the following flexion. These observations support the idea that extensor reflexes elicited from the skin of the distal limb indeed participate in locomotion (see Introduction). The actions from the pad and plantar side of the foot during the stance are essentially twofold: firstly, there is an increase in the intensity of the ongoing extension; secondly, there is a delay in the onset of the flexor activity. Both actions seem particularly useful for an animal walking over an unpredictable surface. An unexpected extra loading of the hindlimb during the stance phase will provide extra stimulation of the cutaneous receptors of the pad or the plantar surface of the foot, and this in turn will lead to a reflexly evoked increase in extensor activity, counteracting the load. Furthermore, the presence of extra stimulation to the pad or the plantar surface of the foot will delay the moment at which the foot is lifted from the ground (swing phase).

The first action, the reinforcement of the extensor activity during the stance, is not exclusively seen after stimulation of the pad or the plantar surface of the foot. Forssberg et al. (1975) observed that stimulation of the dorsum of the foot during the stance phase increased the amplitude of the extension in chronic spinal cats. Thus several skin areas of the distal hindlimb may provide additional extensor excitation during the stance. Possibly this is a remnant of the strong and widespread cutaneous extensor reflexes of the immature kitten. According to Ekholm (1967), the source of the most effective excitation of extensor motoneurons shifts postnatally from cutaneous exteroceptors to muscle proprioceptors, a change which coincides with the development of the gamma motor system. It might then be expected that cutaneous reflexes have evolved to occupy functions in parallel with proprioceptive reflexes, appearing at a later stage. In the adult animal extensor reflexes are indeed readily evoked by stimulating muscle nerves as well as cutaneous nerves (Sherrington and Sowton, 1911). A close parallelism in the actions from exteroceptors and proprioceptors is likely to explain why so little deficit was seen in the experiments with denervation or anaesthesia of the skin of the foot (Sherrington, 1910; Engberg, 1964).

A second effect, resulting from pad and plantar skin stimulation during the stance, concerns the delay of the swing phase. Here the present results differ from the observations of Forssberg et al. (1975) who found that stimulation of the dorsum of the foot during the stance resulted in a shortening of the extensor activity causing an earlier onset of the swing. Possibly such discrepancies reflect fundamental differences in the reflex organization of afferents from different skin areas. For the pad, our data are in line with observations of Perret (1973) who found that light pressure on the pad of paralyzed or non-paralyzed thalamic cats evoked a tonic activation of the extensor motoneurons associated with a block of the rhythmic flexor activity. Both the work of Perret (1973) and the present study indicate that cutaneous afferents from the pad provide inhibition to the neuronal system producing swing. Interestingly, a similar reflex inhibition of the swing generation

has been found recently for muscle afferents (Pearson and Duysens, 1975). Again, this points to the close similarity in reflex effects obtained after stimulation of skin afferents and muscle afferents.

So far only the situation with stimulation during the stance phase has been considered. When stimuli to the pad or plantar surface of the foot were given during the swing, two main features were seen. (i) When stimulation was applied to the plantar surface of the foot very early in the swing a prolongation of the flexor burst was observed, while no change was seen in extensor activity. This is similar to the results of Forssberg èt al. (1975) who found that electrical and tactile stimulation of the dorsum of the foot during the swing phase markedly increased and prolonged the ongoing flexion. Forssberg et al. (1975) suggested that the enhanced flexion could help the animal to overcome a fixed obstacle which touched the dorsum of the limb during the swing. Possibly the prolonged flexion described in this paper could have a similar function but it seems unlikely that obstacles would touch the plantar side of the foot or the pad during the swing phase of a freely moving normal cat. (ii) Most commonly, pad and plantar surface stimulation starting in the swing, had an inhibitory effect on the amplitude and duration of the next extensor burst, leading to a shortening of the step cycle. The inhibition of the extensor activity was coupled to a prolongation of the flexor activity, suggesting an underlying mechanism of reciprocal inhibition. Note also that the extensor inhibition was seen at a moment when the extensors were normally activated during the step cycle.

Some results obtained with skin stimulation could be duplicated using low threshold sural nerve stimulation. In particular both the extensor reinforcing and prolonging effects were seen when weak stimuli were applied during the contraction phase of the ipsilateral triceps surae during locomotion. The similarities with the results obtained by skin stimulation are not surprising since the sural nerve innervates the lateral part of the plantar surface of the foot (Hunt and McIntyre, 1960). Moreover, it is known that low threshold sural nerve afferents have excitatory pathways to both alpha and gamma motoneurons of the ipsilateral triceps surae (Hagbarth, 1952; Eldred and Hagbarth, 1954) and that monosynaptic ankle extensor reflexes are facilitated by volleys in the sural nerve (Bernhard, 1947). The present data suggest that these extensor promoting reflexes from the sural nerve play a role in assisting the ankle extensors during the stance phase of walking.

The demonstration that extensor facilitating pathways are opened during the stance phase and closed during the swing should not be taken as support for the now discarded views of Philippson (1905) who saw walking as a sequence of interlocking reflexes. Rather, the present findings illustrate how the locomotory system provides a means for gating certain cutaneous reflexes, which were suspected by both Philippson (1905) and Sherrington (1910) to be important in locomotion.

References

Bernhard, C.G.: Slow cord potentials of opposite sign correlated to reciprocal functions. Acta physiol. scand. Suppl. 47, 14, 6 (1947)

Ekholm, J.: Postnatal changes in cutaneous reflexes and in the discharge pattern of cutaneous and articular sense organs. Acta physiol. scand. Suppl. 297, 71 (1967)

Eldred, E., Hagbarth, K.-E.: Facilitation and inhibition of gamma efferents by stimulation of certain skin areas. J. Neurophysiol. 17, 59—65 (1954)

Engberg, I.: Reflexes to foot muscles in the cat. Acta physiol. scand. Suppl. 235, 62 (1964)

Forssberg, G.H., Grillner, S., Rossignol, S.: Phase dependent reflex reversal during walking in chronic spinal cats. Brain Res. 85, 103—107 (1975)

Grillner, S.: On the spinal generation of locomotion. In: Sensory organization of movements. (ed. A.S. Batuev) 1973

Grillner, S.: Locomotion in vertebrates: central mechanisms and reflex interaction. Physiol. Rev. 55, 247—304 (1975)

Hagbarth, K.-E.: Excitatory and inhibitory skin areas for flexor and extensor motoneurones. Acta physiol. scand. Suppl. 94, 26 (1952)

Hagbarth, K.-E., Naess, K.: Reflex effects of tetanic stimulation of different afferent fibre-systems in the hindlimb of the cat. Acta physiol. scand. 21, 336—361 (1950)

Hunt, C.C., McIntyre, A.K.: An analysis of fibre diameter and receptor characteristics of myelinated cutaneous afferent fibres in cat. J. Physiol. (Lond.) 153, 99—112 (1960)

Magnus, R.: Some results of studies in the physiology of posture. Lancet 2/1926, 531—536

Orlovskii, G.N., Shik, M.L.: Standard elements of cyclic movements. Biofizika 10, 847—854 (1965)

Pearson, K.G., Duysens, J.: Function of segmental reflexes in the control of stepping of cockroaches and cats. In: Neural Control of Locomotion. (ed. R.E. Herman, S. Grillner, D. Stuart, P. Stein). New York: Plenum Press (In press)

Perret, C.: Analyse des méchanismes d'une activité de type locomoteur chez le chat. Doctoral Thesis, University of Paris 1973

Philippson, M.: L'autonomie et la centralisation dans le système nerveux des animaux. Trav. Lab. Physiol. Inst. Solvay (Bruxelles) 7, 1—208 (1905)

Pritchard, E.A.B.: Die Stützreaktion. Graphische Analyse am Hinterbein der Katze. Pflügers Arch. ges. Physiol. 214, 148—168 (1926)

Schoen, R.: Die Stützreaktion. Pflügers Arch. ges. Physiol. 214, 21—47 (1926)

Sherrington, C.S.: Qualitative difference of spinal reflex corresponding with qualitative difference of cutaneous stimulus. J. Physiol. (Lond.) 30, 39—46 (1904)

Sherrington, C.S.: The integrative action of the nervous system. New Haven, Conn.: Yale University Press 1906

Sherrington, C.S.: Flexion-reflex of the limb, crossed extension reflex, and reflex stepping and standing. J. Physiol. (Lond.) 40, 28—121 (1910)

Sherrington, C.S., Sowton, S.C.M.: Reversal of the reflex effect on an afferent nerve by altering the character of the electrical stimulus applied. Proc. roy. Soc. B 83, 435—446 (1911)

Whitehorn, D., Howe, J.F., Lessler, M.J., Burgess, P.R.: Cutaneous receptors supplied by myelinated fibers in the cat. I. Number of receptors innervated by a single nerve. J. Neurophysiol. 37, 1361—1372 (1974)

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