Differential Effects of Footpad Stimulation on the Monosynaptic Reflex in the Spinalized Cat

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ABSTRACT. Experiments were performed in 17 adult cats spinalized at T10–11. The effects of electrical stimulation of the central pad (CP) and toe pads (TP-2, 3, 4, 5) on the monosynaptic reflex (MR) in lumbar spinal segments were studied. The conditioning stimulation had different effects on the MRs of the various motoneurons except the posterior biceps and semitendinosus, depending on the footpad stimulated. Lateral gastrocnemius and soleus, and medial gastrocnemius (MG) MR were inhibited by footpad stimulation. The effect of TP-2 (medial footpad) stimulation on MG-MR was weak. The popliteus (Pop) and tibialis anterior muscles (TA) are inward and lateral rotators of the knee joint, respectively. Pop- and TA-MR were excited by stimulation of lateral and medial TPs, respectively. Plantaris MR was enhanced and inhibited by stimulation of the CP and TPs, respectively. There were remarkable differences in the effects of TP conditioning stimulation on the flexor digitorum longus, extensor digitorum longus, peroneus brevis and teritius, and peroneus longus-MRs, depending on the toe pads stimulated. These results suggest that afferent inputs from footpads modulate the activity of motoneurons, stabilize the foot and help maintain body balance.—**KEY WORDS:** feline, footpad, hindlimb, monosynaptic reflex, spinal cord.

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When cats stand, walk or run, footpads on the plantar surface of the feet come in contact with the ground. Engberg [2] reported that motoneurons innervating short plantar muscles are activated by gentle pressure on the footpads. Mori *et al.* [8] reported that loss of afferent activity from the feet produces minor but detectable deficiencies in the control of posture. Recently, Hongo *et al.* [3] showed that plantar muscles (interosseus muscles) are activated by pressure on the footpads, and that the effects of toepad pressure on muscle activity depends on the footpad stimulated. They suggested that afferent inputs from footpads control foot stability. To understand the physiological role of afferent information from footpads, their studies are not sufficient. In the present experiments, the effect of footpad stimulation on the monosynaptic reflex of various hindlimb motoneurons was studied in the spinalized cat.

MATERIALS AND METHODS

Experiments were performed on 17 adult cats, weighing 2.2–4.2 kg. The cats were anesthetized with an intraperitoneal injection of 10% urethan (500 mg/kg) and 1% alpha-chloralose (50 mg/kg). The spinal cord was transected at T10–11. The animal was immobilized with gallamine triethiodide, and artificially ventilated. The End-tidal CO₂ concentration was monitored and maintained close to 4% by adjusting the tidal volume or ventilator rate. Arterial blood pressure was monitored through a catheter inserted into the common carotid artery and was normally above 80 mmHg. Rectal temperature was monitored with a thermometer (YS1, 43TA) and maintained at approximately 37±1°C with an infrared lamp.

The L7 and S1 ventral roots were cut and the central cut end of the L7 ventral root was mounted on a pair of silver

electrodes for recording. The following hindlimb muscle nerves were cut and mounted for stimulation: posterior biceps and semitendinosus (PBSt), medial gastrocnemius (MG), lateral gastrocnemius and soleus (LGS), plantaris (PI), popliteus (Pop), flexor digitorum longus (FDL), tibialis anterior (TA), peroneus longus (Per l), peroneus brevis and teritius (Per. b+t), extensor digitorum longus (EDL) and the plantar section of the tibial nerve (Tib). Each nerve was electrically stimulated with a single pulse (0.1 ms duration) to induce monosynaptic reflex (MR). The strength of the stimulus was adjusted to five times the threshold, determined from an incoming volley recorded with a monopolar electrode on the L6 or 7 dorsal root. The footpads were electrically stimulated through needles inserted into each footpad. Figure 1B shows the arrangement of the footpads. The intensity of the electrical stimulation was adjusted to five times the threshold and the intervals between test stimulation of the muscle nerves and conditioning stimulation of the foot pad were set at 10, 20, 30, 40, 50, and 100 ms. Eight MRs recorded from the L7 ventral root were averaged by means of a signal processor (7T17 NEC-Sanei). The magnitude of the MR was defined as the area enclosed by the action potential averaged. The effect of conditioning stimulation on MRs was expressed in terms of percent control. Kuno [6] reported that the inhibitory effects depended on MR size. Therefore, when MR size fluctuated or was small, the data were eliminated. Quantitative differences in the degree of the conditioned stimulus effect on MR were examined for significance by Student's *t*-test.

RESULTS

Figure 1A illustrates the effects of stimulation of CP, TP-5 and TP-2 on the MG monosynaptic reflex at 10, 20, 30, 40, 50, and 100 ms intervals. MG-MR was inhibited by

Fig. 1. A, Effects of the conditioning stimulus of the CP, TP-5 and TP-2 on the MG monosynaptic reflex at 10, 20, 30, 40, 50 and 100 ms intervals. Upper and lower traces show averaged MG monosynaptic reflex and incoming volley, respectively. In the column on the far left, the unconditioned MG-MR are shown. The vertical bar at the bottom on the right side is 1.0 mV in the upper traces (MRs) and 0.5 mV in lower traces (incoming volley). Note that the strength of the inhibitory effects of conditioning stimulation of footpads depends on the footpads stimulated and the intervals. B, the arrangement of footpads.

Fig. 2. Effects of electrical stimulation of footpads on the monosynaptic reflex of various hindlimb motoneurons. Each dot indicates the mean for 7 experiments, and the vertical bars indicate the standard deviation. Horizontal axis; the interval between the conditioning stimulation of the footpad and the test stimulation of the muscle nerves (ms). Vertical axis; degree of the effects of the conditioning stimulation (control %). PBSt: posterior biceps and semitendinosus, MG: medial gastrocnemius, LGS: lateral gastrocnemius and soleus, PI: plantaris, Pop: popliteus, FDL: flexor digitorum longus, TA: tibialis anterior, EDL: extensor digitorum longus, Per. l.: peroneus longus, Per. b+t: peroneus brevis and teritius, Tib: the plantar section of the tibial nerve. Note that the effects of footpad stimulation depend on the kind of motoneurons and the footpads stimulated.

stimulation of the footpad, but the degree of inhibition was different depending on the footpads stimulated and the intervals.

Figure 2 shows the effect of electrical stimulation of the footpad on the monosynaptic reflex of various hindlimb motoneurons.

PBSt-MR was facilitated by the conditioned stimulus of footpads at 10–30 ms intervals. At 50 and 100 ms intervals, a weak inhibition was observed. This inhibition was not statistically significant, except for CP stimulation at 50 ms intervals ($p < 0.05$).

The MG-MR was inhibited by stimulation at 10–20 ms intervals. The inhibitory effect of the conditioning stimulation of the lateral toe pads (TP-4, 5) tended to be stronger than that of medial toe pad (TP-2, 3) stimulation.

LGS-MR was inhibited by the conditioning stimulation of CP and TPs at 10–30 ms intervals. The degree of the effect did not depend on the TP stimulated.

PI-MR was enhanced by CP stimulation at 10–20 ms intervals, and inhibited by conditioning stimulation of TPs.

Pop-MR was enhanced by the conditioning stimulation of CP and TPs. The strength of the effects of TP stimulation on Pop-MR depended on the footpad stimulated. When the conditioned stimulus was changed from the lateral to the medial TP, the effect was weakened, and the effects of TP-5, 4 and TP-2, 3 stimulation at 20–50 ms intervals differed statistically ($p < 0.05$).

FDL-MR was enhanced by CP stimulation, while the effect of TP stimulation varied with the TPs stimulated. The conditioned stimulus effects changed from facilitation to inhibition at 10 and 20 ms intervals when the stimulated TP changed from TP-5 to TP-2.

TA-MR was inhibited by CP and lateral TP (TP-4 and

5) stimulation and facilitated by medial TP (TP-2 and 3) stimulation at 10–30 ms intervals.

EDL-MR was enhanced by CP stimulation, while the effects of TP stimulation were not marked.

Per.l-MR was enhanced by CP stimulation at 10–30 ms intervals. The degree of the effect of TP stimulation differed depending on the TPs stimulated. Facilitation by TP stimulation at 10–50 ms intervals weakened when the stimulated TP changed from TP5 to TP2. The effects of TP-5 and TP-2 stimulation differed statistically at 10 ms intervals ($p < 0.05$).

In Per.b+t-MR, the interval-effect curve for TP stimulation shifted from facilitation to inhibition when the stimulated TP was changed from TP-5 to TP-2.

Tib-MR was facilitated by CP stimulation at 10–30 ms intervals. The effect of TP stimulation was not statistically significant at 10–40 ms intervals.

DISCUSSION

In spinal animals under static conditions a flexor reflex pattern prevails, i.e. the excitatory pathway to flexors, the PBSt-MR, is activated, while the excitatory pathways to extensors, the LGS- and the MG-MRs, are inhibited. The effect on the MG-MR depended on which toepad was stimulated, but the effects on the LGS-MR did not depend on the toepads stimulated. These data indicate differences in neuronal connection to the MG and the LGS motor nuclei, from cutaneous nerves innervating the footpads. Labella *et al.* [7] reported differences in the synaptic input to the MG, LG and Sol from cutaneous sural nerves, i.e., stimulation of caudal cutaneous sural nerves preferentially excites MG motoneurons. In this study, such excitatory effects were also observed for the MG-MR. This difference in effects on the MG- and LGS-MRs suggests a functional difference between these muscles. Some reports indicate differential activation of the triceps surae. Nardone and Schieppati [9] reported selective MG inhibition during cyclic ankle plantar and dorsi flexion in humans. Smith *et al.* [10] reported that in the cat, during rapid paw shakes only the gastrocnemius, but not the soleus, motoneurons were activated.

Studies on the P1-MR indicate that the foot is extended when CP receptors are stimulated, and flexed when TP receptors are stimulated. These footpad reflexes stabilize the foot, as indicated by Engberg [2].

Pop contraction causes inward leg rotation and shank flexion. Our results indicate that when the lateral toe pad receptors are stimulated, the Pop rotates the leg inward to stabilize the foot. In contrast to Pop, the TA rotates the leg outward. These results suggest that afferent inputs from the footpad control foot stabilization.

FDL contraction flexes the digits and extends the foot, and its different functions in different digits have not been reported. However, the effects depended on the footpads stimulated. In EDL-MR (digits extensor and foot flexor), the effects depended on which footpad was stimulated. Further studies are needed to explain the effects of footpad stimulation on FDL and EDL-MRs.

Per. b. extends the foot and Per. l and t flex it. Furthermore, Per. l rotates the foot and Per. t extends digit V. When the CP was stimulated, the effect on these monosynaptic reflexes followed a flexor reflex pattern. When the stimulation was performed from TP-5 to TP-2, the effect-interval curve shifted from facilitation to inhibition. Further study is required to understand the results of the Per. l. and Per. b+t reflexes.

The plantar portion of the Tib nerve innervates various muscles, including the Mm interosseus, and abductor digit quint II-V. Hongo *et al.* [3] showed that the degree of electromyographic activity of the interosseus muscle

depended on which TP was stimulated. Since the effects on Tib-MR included effects on the MR of various motoneurons, and these effects differed, the effects of the stimulation may have been weak.

As a cat moves or maintains a posture, afferent inputs from various types of receptors change from moment to moment. Our results indicate that inputs from receptors in the footpads convey information regarding foot condition, and that afferent inputs from footpads modulate the activity of motoneurons in the various hindlimb muscles, adapting to changes in foot condition. In this study, electrical stimulation of footpads was performed to observe the typical patterns of the effects of afferent inputs from footpads. Janig *et al.* [4, 5] and Behrends *et al.* [1] showed different types of receptors in the footpad. The effect, on MR, of different types of sensory receptors in the cat footpads needs further study.

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