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Pyramidal Tract Control over Cutaneous and Kinesthetic Sensory Transmission in the Cat Thalamus

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Summary. In the thalamic ventrobasal complex (VB) of the cat, effects of electrical stimulation of the pyramidal tract (PT) upon activities of 112 relay cells and 18 internuncial cells were examined. Single PT shocks to the cerebral peduncle elicited short-latency discharges in 31 relay cells (mean latency, 1.4 ± 0.5 msec). When weak PT stimuli were employed as conditioning shocks, facilitatory effects upon responses to medial lemniscal (ML) stimulation were observed. It was revealed that VB relay cells were excited monosynaptically via collaterals of the fast PT fibers. Among 31 PT-excited cells 22 were fired by movements of joints (joint-movement units) and they made up 88% of all the joint-movement units. A majority of the relay cells responding to stimulation of hairs (hair units) did not receive excitatory effects from PT, except some special ones which represented long hairs at the distal or proximal end of the forearm-forepaw.

In 44 relay cells repetitive PT shocks suppressed both evoked responses to ML stimulation and spontaneous discharges for 70—100 msec. Of these, 34 were hair units. The PT-induced inhibition in the hair units increased as their receptive fields shifted from the trunk towards the digits. Some intracellular recordings showed that the PT-induced inhibition was due to IPSPs generated disynaptically.

Among 18 interneurons presumed to be inhibitory 10 responded with short latencies to PT stimulation. These were mostly the interneurons which presumably subserve the recurrent collateral inhibition in VB.

Key words: Ventrobasal thalamus — Cutaneous sensation — Kinesthesia — Pyramidal tract control

Introduction

Several studies have reported that the sensorimotor cortex (SMC) of the cat exerts some regulatory influence upon afferent transmission in the thalamic ventrobasal complex (VB) (Ogden, 1960; Iwama and Yamamoto, 1961; Andersen *et al.*, 1972; Burchfiel and Duffy, 1974). Such a corticothalamic sensory control has been categorized as facilitatory (Andersen *et al.*, 1972), inhibitory (Ogden, 1960; Burchfiel and Duffy, 1974) or both (Iwama and Yamamoto, 1961). In 1965 Shimazu and his associates found that upon stimulation of the pyramidal tract (PT) at the medullary pyramid, a substantial number of VB relay cells were

either excited or inhibited. They suggested that at least a part of the corticothalamic sensory control is mediated through PT fibers sending branches to VB.

The present investigation was aimed to elaborate some details of the PT control upon sensory transmission in VB. Effects of electrical stimulation of PT fibers were examined in individual VB neurons which were classified with respect to the types of natural stimuli most effective in activating them. It was found that the predominant effect of PT control was facilitatory in the VB relay cells mediating kinesthesia and inhibitory in those mediating cutaneous sensation.

Methods

Activities of VB neurons were recorded in 17 adult cats. Initially they were anesthetized with Nembutal (30 mg/kg) given intraperitoneally. To keep the animals at a moderate level of anesthesia further administration of the same anesthetic was made by the method of drip infusion through a polyethylene tube inserted into the femoral vein. Furthermore, the animals were paralyzed with Flaxedil (4—5 mg/kg) and artificially ventilated.

Responses of VB units to single shock stimulation of the medial lemniscus (ML) and SMC were examined to determine whether the units were relay or internuncial cells based upon the criteria proposed by Andersen *et al.* (1964a) and supported by Tsumoto and Nakamura (1974). For ML stimulation two bipolar electrodes, each consisting of two insulated wires aligned singly with bared tips about 1.5 mm apart, were inserted stereotaxically into two points of ML. The stereotaxic coordinates of the sites of ML stimulation were L 3.0 and H —7.5 at F —1, and L 0.5 and H —10.5 at F —11. For SMC stimulation 8—12 bipolar electrodes were burried around the cruciate sulcus, both anteriorly and posteriorly to it. For each of ML and SMC stimulation one electrode was selected to activate VB units with minimum intensity. Such stimulation was made by applying single pulses of 0.01—0.05 msec duration with the protruded electrode tip as cathodal.

To classify VB units in terms of most effective natural stimuli, responses were observed by applying different types of natural stimuli to skin, joints and subcutaneous tissues in various parts of the body. All these observations were carried out in the same way as described by Tsumoto (1974).

For stimulation of PT a bipolar electrode of the same type as applied to ML was inserted into the cerebral peduncle stereotaxically. The position of the electrode was adjusted according to the maximal amplitude of mass responses of PT fibers following single shock stimulation of SMC. The stereotaxic coordinates of the site of peduncular stimulation were L 4.0 and H —6.0 at F +5.0. This stimulation site will be called PT_p. In some experiments PT was stimulated at two separate sites, one at PT_p and the other close to the junction of the medullary pyramid and the trapezoid body. The latter stimulation point will be called PT_m. It was approached ventrally by cutting the basioccipital bone. PT stimulation was made with a single pulse of 0.01—0.05 msec duration or with a train of 5 pulses at 500 Hz.

Jabbur and Towe (1961a) established that only the early waves, a and β, of SMC responses evoked by PT stimulation could be attributed to antidromic impulses of PT and that the b—d waves evoked by strong PT stimulation were due to orthodromic impulses of ML. We used Jabbur and Towe's finding as a criterion to control the intensity of PT stimulation and adjusted it to usually 80—90% of the threshold of b—d waves. According to Takahashi (1965) this intensity of PT stimulation was enough to activate the slow as well as fast PT fibers.

Excitatory influences of PT upon VB neurons were examined by observing whether spike discharges were evoked with short latency by single shock stimulation of PT. In the units which were found not excited at short latency by single shock stimulation of PT, the possibility that PT stimulation exerted inhibitory effects upon them was examined by applying 5 shocks at 500 Hz. The PT-induced inhibition was identified as depression of ML-evoked discharges and spontaneous discharges. The depression of spontaneous discharges was ascertained from poststimulus time histograms (PSTHs). In some experiments intracellular recordings from VB neurons were made in order to observe IPSPs as a sign of PT-induced inhibition. The criteria for intracellular recordings have been described in a preceding paper (Tsumoto and Nakamura, 1974).

At the end of the experiments, in 12 cats, lesions were made through PT electrodes by passing a current of about 1 mA for 1 min. The animals were then sacrificed by an overdose of Nembutal, the brains fixed with 10% formalin and the tips of PT electrodes located. In 4 cats, in which electrodes were introduced to PT_p and PT_m, the distance between the two stimulation sites was measured. It was 12.4 ± 0.6 (S.D.) mm in average.

Results

Recordings were made from 112 VB relay cells and 18 internuncial cells which were held long enough to observe response characteristics following natural stimuli and to examine the effect of PT stimulation upon them. The second column of Table 1 gives a classification of these 112 relay cells according to the types of most effective natural stimuli (Tsumoto, 1974). The distribution of the unit types is approximately the same as that of 230 relay cells in Tsumoto's report (1974), except that the subcutaneous-distortion and hair-suppressed units which constituted a minor group of VB relay cells were not encountered.

Primary Excitation of Relay Cells by PT Stimulation

Among a total of 112 VB relay cells, 31 cells responded to PT stimulation with short latencies. These cells will be called "PT-excited cells". An example of responses of a PT-excited cell is shown in Fig. 1. This unit was activated by flexion of the ankle joint (see top right of the figure) and had stable responses to ML stimulation (B). PT_p stimulation elicited spike discharges with short latencies of 1.2 ± 0.1 msec in average (A). The variation in response latency to PT_p stimulation was a little larger than that to ML stimulation (compare A and B). When a PT_p shock of subthreshold intensity preceded a testing ML shock by 2 msec, the latency of the ML-induced response was reduced by about 0.5 msec and the response probability increased to 100% (C).

The time course of PT-induced facilitation is shown in Fig. 1D where the response probability and the response latency to testing ML stimulation are shown as functions of the interval between conditioning PT_p and testing ML stimulation. The response probability, which was 55% in the control stage, increased to 100% at the conditioning-testing interval of 2 msec. Associated with this the response latency was maximally decreased. The total duration of the facilitatory effect was 5 msec in this case. The longest duration of the facilitation observed in this experiment was about 10 msec.

In 31 relay cells the mean response latency to PT_p stimulation was 1.4 ± 0.5 msec. This value suggests that the excitatory input to VB relay cell is mediated monosynaptically. A direct support for this presumption was obtained from 11 relay cells in which stimulation was applied to both PT_p and PT_m. In each cell the response latency for PT_m stimulation was longer than that for PT_p stimulation. From the pairs of latency values and the conduction distance, the synaptic delay at VB was estimated by the graphical method shown in Fig. 2, assuming that the conduction velocities of PT fibers remained unchanged from PT_m to the axon terminals of PT collaterals. The mean synaptic delay at VB in 11 relay cells was 0.90 ± 0.08 msec. This indicates that only one synapse is involved in the pathway from terminals of PT collaterals to VB relay cells.

From the same 11 relay cells, conduction velocities of PT fibers which carried excitatory impulses to them were calculated as the distance between PT_m and

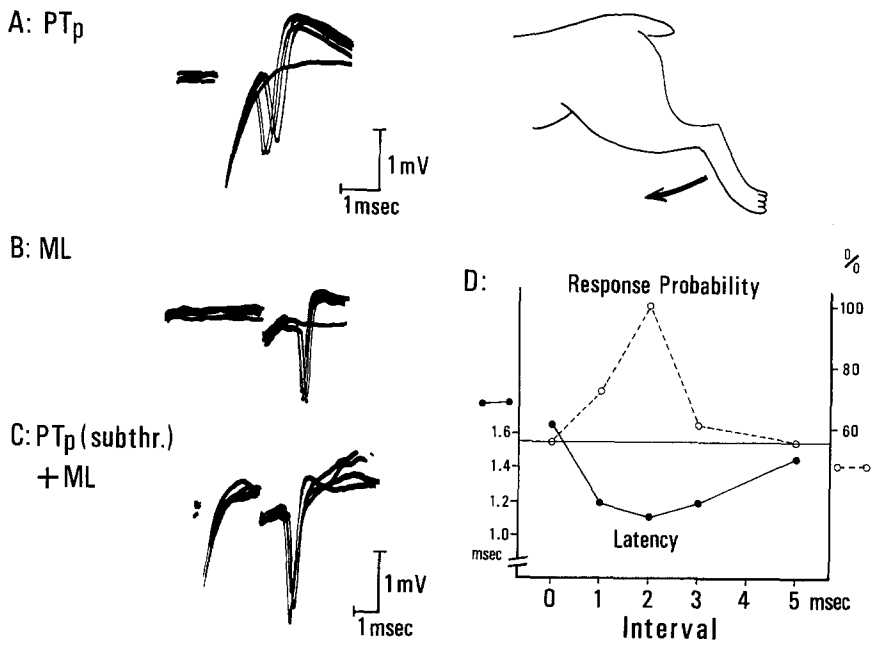

Fig. 1. PT-evoked responses of a VB relay cell and facilitatory effects of PT stimuli upon ML-evoked responses. In the top right the arrow shows flexion of the ankle joint which was most effective to activate this unit. (A) Responses to single shocks applied to the cerebral peduncle. (B) Responses to single shocks applied to ML. Stimulus intensity, about twice the threshold. (C) The same as in B, except that PT stimuli of a slightly subliminal intensity preceded ML shocks by 2 msec. The time scale in C applies to B. (D) Time courses of PT facilitation. Abscissae, intervals between ML and PT stimulation. Filled circles, response latencies to testing ML stimulation. Open circles, response probabilities to testing ML stimulation. A horizontal line indicates control values of response latency and probability

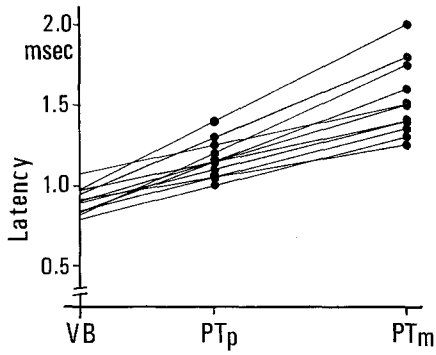

Fig. 2. Synaptic delays at VB for PT-induced excitation. A pair of dots connected by a line represents latency values of responses to PT_p and PT_m stimulation for each unit. Abscissa indicates conduction distance. The distance from VB to PT_p was calculated as 8.6 mm from the stereotaxic coordinates of the two sites. The average recording site in VB, L 7.0, H +1.0 and F +9.0. For stereotaxic coordinates of PT_p, see Methods. The distance from PT_p to PT_m was measured as 12.4 mm (see Methods)

PT_p divided by the differences in response latency. For each stimulation the response latency was averaged over 20 consecutive responses. The velocity is distributed in the range from 21 to 62 m/sec with a mean value of 38 ± 13 m/sec. This indicates that the VB relay cells were excited by the fast PT fibers defined by Takahashi (1965).

The distribution of 31 PT-excited cells according to the types of most effective natural stimuli is shown in the third column of Table 1, along with the same

Table 1. Classification of VB relay cells receiving primary excitation, inhibition and no effect from PT

Types of adequate stimuli	No. of units	Excited units	Inhibited units	Non-affected units
Joint-movement	25	22 (88%)	3 (12%)	0 (0%)
Hair	71	8[a](11%)	34 (48%)	29 (41%)
Pressure	5	0 (0%)	3 (60%)	2 (40%)
Pad-touch	5	0 (0%)	2 (40%)	3 (60%)
Claw-movement	6	1 (17%)	2 (33%)	3 (50%)
Total	112	31 (28%)	44 (39%)	37 (33%)

[a] of 8 units, six were categorized as extraordinary hair units. See details in text.

classification of the total 112 cells. Of 31 PT-excited units, 22 were joint-movement units; they constituted 88% of the total sample of joint-movement units. On the other hand, the hair units were rarely excited by PT stimulation except for a small number of units of which a detailed description will be given below. Although the scarcity of samples of the other types of units did not allow us to draw a definitive conclusion, it is to be noted that none of the pressure and pad-touch units which may subserve cutaneous sensation together with the hair units were excited by PT stimulation.

Extraordinary Hair Units Excited by PT Stimulation

In a previous paper Tsumoto (1974) described some hair units as extraordinary, because they represented a few long hairs of tips of the forepaw-digits and were innervated by ML fibers having much faster conduction velocities than for the ordinary hair units representing the digits. In the present study six of the eight PT-excited hair units were categorized as extraordinary. Among the six extraordinary hair units, four represented a few hairs of the tips of forepaw-digits and two those of the skin covering the olecranon of the elbow. Their hairs were characterized by conspicuously long and thick shafts.

In these extraordinary hair units the response pattern to ML and SMC stimulation differed from each other. An example is shown in Fig. 3. This unit was easily activated by very slight movements of a few long hairs of the tip of the fourth forepaw-digit (see top right of the figure). The response was fast adapting as is the case in the ordinary hair units. PT_p stimulation elicited consistent responses of single spikes with a latency of 1.1 msec (A). To ML stimulation this unit responded with a single spike with a latency of 1.2 msec (B). On the other hand, SMC stimulation yielded repetitive responses of 4—6 spikes of which the first one was an antidromic spike and the others were orthodromic ones.

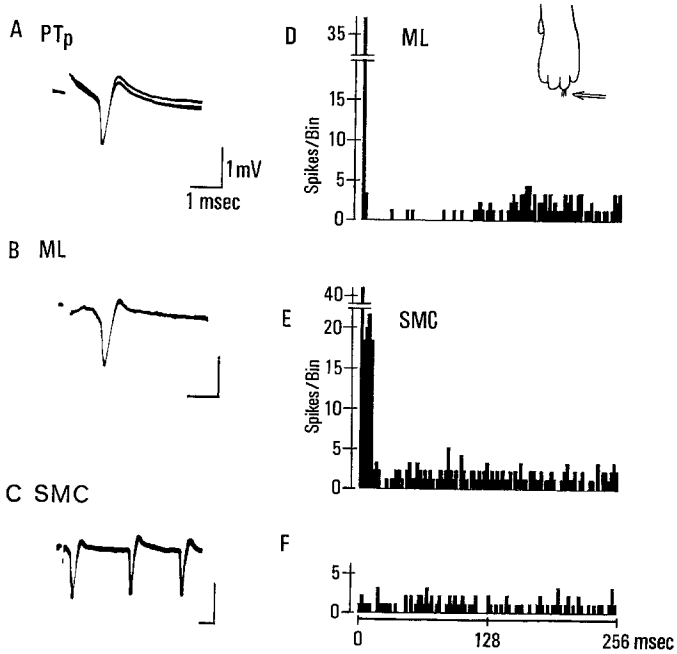

Fig. 3. Responses and time histograms recorded from an extraordinary hair unit. The arrow in the inset figure in the top right shows that this unit responded to movements of a few long hairs on the tip of the fourth forepaw-digit. (A—C) Responses to single shocks applied to the site indicated in each record. A and B two sweeps were superimposed. (C) Single sweep. D and E are PSTHs after stimulation of the sites indicated in each histogram. Number of sweeps, 100. F is a time histogram for spontaneous discharges made under the identical condition for the same unit without stimulation

Another important difference in the response patterns for ML and SMC stimulation was revealed by compiling PSTHs (D and E). In D, ML stimulation yielded depression of the spontaneous discharge (discharge depression, see Tsumoto and Nakamura, 1974) for about 100 msec after the short-latency discharges, while in E SMC stimulation resulted in only a very faint discharge depression after the antidromic discharges. This is in contrast with the fact that in ordinary hair units the strength of discharge depression following ML stimulation is about the same as that following SMC stimulation (Tsumoto and Nakamura, 1974).

Primary Inhibition of Relay Cells by PT Stimulation

Primary inhibition means the inhibition that occurs without being preceded by excitation (Creutzfeldt *et al.*, 1966). This type of inhibition was seen in 44 units (PT-inhibited units). An example of a PT-inhibited unit is shown in Fig. 4. This unit responded to movements of hairs in a region near the wrist (see top middle of the figure). In response to ML stimulation this unit fired consistently with a fixed latency (A). When ML stimulation was preceded by repetitive shocks, the response probability to ML stimulation was reduced and the response latency

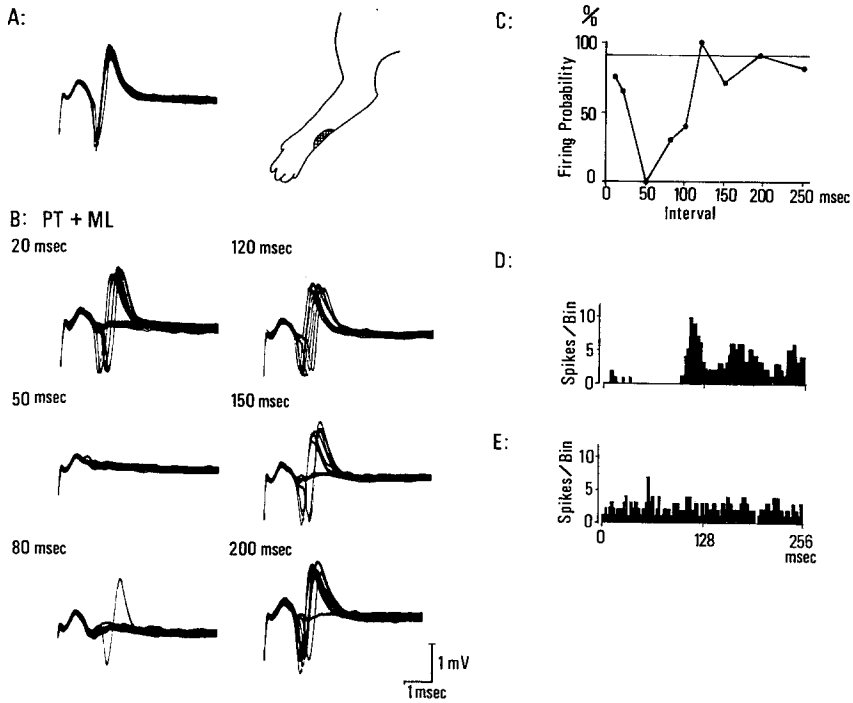

Fig. 4. PT-induced inhibition of a VB relay cell. Inset in the middle top shows that this unit responded to stimulation of hairs on the hatched area. (A) Responses to single ML stimuli. Stimulus intensity, about 3 times the threshold. Superimposition of 10 sweeps. (B) ML stimuli of the same intensity as in A were preceded by 5 PT shocks at 500 Hz as conditioning stimuli. Intervals between ML shock and the first shock of PT are indicated in each record. Superimposition of 10 sweeps. (C) Time course of inhibitory effects of PT stimulation upon ML-evoked responses. Abscissae, intervals between PT and ML shocks. Ordinates, firing probabilities of responses to testing ML stimuli. A horizontal line indicates the control value of response probability. (D) A PSTH made by PT stimuli of 5 shocks. Sweeps started simultaneously with the first PT shock. Number of sweeps. 100. (E) A time histogram for spontaneous discharges made under the identical condition for the same unit without stimulation

prolonged (B). The inhibitory effects of PT stimulation was obvious at an conditioning-testing interval of 20 msec and most marked at 50 msec. At an interval of 120 msec a complete recovery of responsiveness was observed. The entire time course of the PT-induced inhibition is shown in Fig. 4C where the response probability to ML stimulation is shown as a function of time after the onset of conditioning PT shocks. As shown in the PSTH of Fig. 4D, PT repetitive stimuli also depressed the spontaneous discharge of this unit. The discharge depression was almost complete for 90 msec after PT stimulation and it was followed by rebound discharges peaking at around 110 msec. The time course of the PT-induced inhibition on the spontaneous discharges was quite similar to that which acted onto the ML-evoked discharge.

Intracellular recordings from several hair units indicated that the PT-induced depression of spontaneous and ML-evoked discharges was most likely due to IPSPs. Records of Fig. 5 were obtained from a hair unit with a restricted RF on

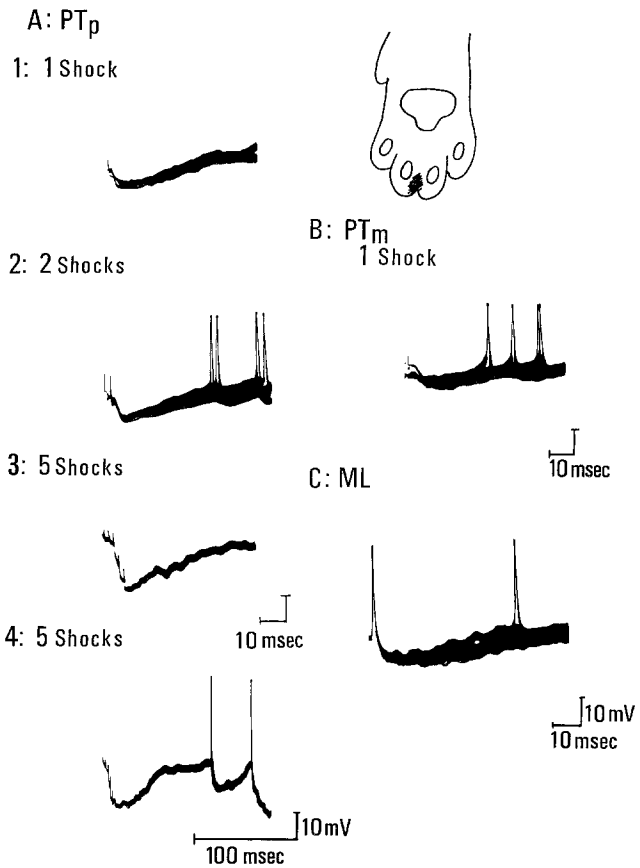

Fig. 5. Intracellular records from a hair unit. In the inset in the top right the receptive field of this unit is shown with hatches. (A) Responses to PT_p stimulation. Number of shocks applied to PT_p are indicated in each record. In all records, except A-3 and -4, five sweeps were superimposed. (B) Responses to PT_m stimulation. (C) Responses to ML stimulation

the palmar side of the interdigital area between the third and fourth forepaw-digits (see top right of the figure). This unit showed a resting membrane potential of about 55 mV. When single shocks were applied to PT_p, recognizable hyperpolarizations were elicited (A-1). Since these hyperpolarizations were not preceded by spike discharges, they are IPSPs. The latency of the IPSP was 2.1 msec and the duration was about 40 msec. When the number of PT shocks increased from one to two and further to five, a corresponding increase in the peak amplitude and duration of the IPSPs was observed (A1—4). IPSPs of about 15 mV in peak amplitude and of about 60 msec in duration resulted from 5 shocks. Single shock stimulation of ML also elicited IPSPs which were as large as those caused by 5 PT shocks (C).

In the unit of Fig. 5, IPSPs were elicited by stimulation of PT_m as well as PT_p (Fig. 5B). The latency of the IPSP to PT_m stimulation was 2.8 msec. This

value was 0.7 msec longer than that to PT_p stimulation. From these latency values the conduction velocity of PT fibers responsible for the IPSP was calculated as 17.7 m/sec. In another unit the same calculation yielded 24 m/sec. These velocities were smaller than those of the PT fibers exciting VB relay cells monosynaptically (mean, 38 m/sec). For the two PT-inhibited units the synaptic delays at VB were estimated as 1.7 and 1.8 msec by the graphical method. From these values only one interneuron between the PT fibers and the VB relay cells can be postulated.

In two other PT-inhibited units, which were of the hair type, IPSPs were recorded only for PT_p stimulation. In these units the latencies of IPSPs were 3.0 and 3.5 msec. In order to calculate synaptic delay times from these values it was assumed that the IPSPs were generated by PT impulses conducted with the velocity which is slowest in Takahashi's (1965) data (11 m/sec). This assumption leads us to estimate the shortest values of the synaptic delay, i.e., the minimum number of synapses involved. The synaptic delays were calculated as 2.4 and 2.9 msec, respectively. These values suggest that IPSPs of some hair units were generated by impulses through more than, one possibly three synapses.

In the fourth column of Table 1 44 PT-inhibited units are classified according to the types of most effective natural stimuli. It is remarkable that the PT-induced inhibition is apparently rare in the joint-movement units and more common in

Table 2. RF location of hair units receiving primary inhibition from PT

Location of RF	Inhibited units	Total samples	Ratio
Trunk	1	12	8%
Hind limb + Tail	1	4	25%
Hind paw + digits	4	9	44%
Forelimb	14	21[a]	67%
Forepaw + digits	14	19[a]	74%
Total	34	65	52%

Trunk includes neck, back, chest and abdomen. [a] not including extraordinary hair units.

the hair and pressure units. Table 2 shows the distribution of the PT-inhibited hair units with regard to the location of RFs. It can be seen that the ratio of the number of PT-inhibited units to the number of hair units in each RF group increases as the RFs shift from the trunk towards the tips of the limbs.

Responses of Interneurons Presumed to be Inhibitory

In studies on the inhibitory mechanism in VB, the non-relay cells responding with repetitive discharges to ML stimulation were presumed to be inhibitory interneurons (Andersen *et al.*, 1964a). Criteria for presumed inhibitory interneurons were described by Tsumoto and Nakamura (1974). They divided the inhibitory interneurons into two groups (A and B) according to the length of synaptic delay at VB: Group A interneurons with a monosynaptic delay at VB and Group B interneurons with at least a disynaptic delay. In the present study 18 units were identified as inhibitory interneurons. Eight units were classified as interneurons

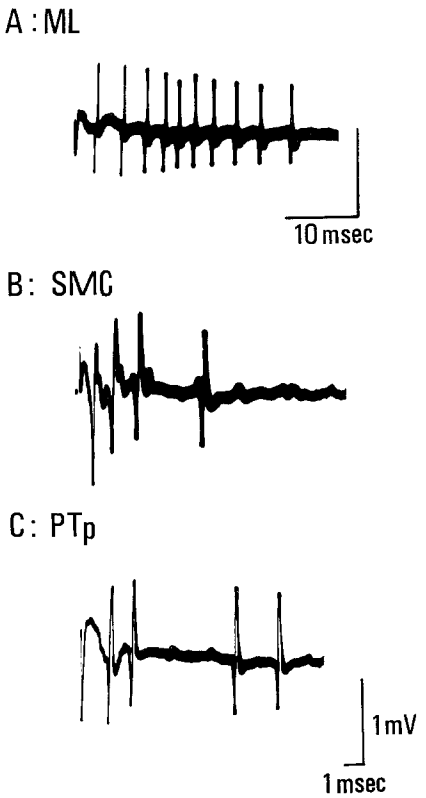

Fig. 6. Responses of an interneuron presumed to be inhibitory. Stimulus sites are indicated in each record. Sweep speed in B is the same as in C

of Group A and 10 of Group B. A total of 10 interneurons were found to respond repetitively to single shock stimulation of PT and 8 of these 10 PT-excited interneurons belonged to Group B.

An example of a Group B interneuron is shown in Fig. 6. This unit discharged repetitively with 8—10 spikes in response to ML stimulation (A). SMC stimulation yielded repetitive discharges of 3—4 spikes (B). PT_p stimulation also elicited repetitive responses (C). The latency of the first spike response to PT_p stimulation was 1.7 msec. The mean latency of the first spike of the repetitive discharge to PT_p stimulation was 1.9 ± 0.6 msec for 9 interneurons, except the tenth interneuron which had a latency of 7.6 msec.

Discussion

Monosynaptic Excitation of the Joint-Movement Units

The present study has shown that about one fourth of the VB relay cells are excited with short latencies by PT stimulation. This coincides with the previous observation of Shimazu *et al.* (1965) that about 29% of VB neurons were excited with short latency by medullary PT stimulation. This PT-induced excitation of

VB neurons did not result from excitation of the dorsal column nuclei (DCN) (Magni *et al.*, 1959; Jabbur and Towe, 1961b; Gordon and Jukes, 1964; Winter, 1965; Towe, 1973), since in 11 VB relay cells the response latencies to PT_m stimulation were consistently longer than those to PT_p stimulation for each of them. Therefore, DCN were not involved in the pathway for primary excitation of VB neurons by PT stimulation. Measurements of the synaptic delay indicated that the PT-induced excitation is caused monosynaptically. This is supported by the finding that the facilitatory effect of weak PT stimulation upon VB transmission is only transient, lasting for not more than 10 msec.

Primary Inhibition of the Hair Units

Our observation that the onset latencies of IPSPs to PT_p stimulation were shorter than those to PT_m stimulation offers a reasonable ground for disregarding the possibility that the inhibitory effects upon VB neurons are derived secondarily from the inhibitory effects upon DCN neurons (Dawson, 1958; Towe and Jabbur, 1961; Chambers *et al.*, 1963; Andersen *et al.*, 1964b, c; Gordon and Jukes, 1964; Levitt *et al.*, 1964; Winter, 1965; Towe, 1973).

Shimazu *et al.* (1965) found that in about one third of VB neurons PT stimulation caused a "delayed inhibition" which ended within 50—70 msec after the stimulation. They suggested that the inhibition seen after conditioning PT stimulation may be attributed to a secondary effect of PT impulses exerted upon VB neurons. This suggestion, however, is not compatible with our conclusion that some VB relay cells were found to receive inhibition from PT collaterals via one inhibitory interneuron only.

The non-relay cells which responded to single PT shocks with repetitive discharges were presumed to be inhibitory interneurons mediating IPSPs to VB relay cells. It was remarkable that most of them were Group B interneurons which were claimed by Tsumoto and Nakamura (1974) to be inhibitory interneurons for recurrent inhibition of the hair units. They found a somatotopic gradient in the strength of recurrent inhibition among the hair units; the inhibition became stronger as RFs of hair units shifted from the trunk towards the limbs. Corresponding to this, the present experiments have revealed that PT-induced inhibition in hair units becomes stronger as their RFs shift peripherally. It appears that Group B interneurons serve to distribute the recurrent inhibition for the hair units on one hand and to mediate the PT-induced inhibition on the other.

Functional Significance of PT Control over Somatosensory Transmission in VB

Wiesendanger (1969) has noted that the PT system forms feedback circuits by sending collaterals to various relay nuclei along its descending courses. In this context it is possible to interprete the monosynaptic connection of PT collaterals to some VB neurons as one of the feedback pathways. Our observation that fast PT fibers were responsible for PT-induced excitation of VB relay cells may be consistent with Wiesendanger's description that the positive feedback mechanism is mediated by fast PT fibers.

According to Andersson *et al.* (1966) neurons in a central nucleus of VB are mainly innervated by somatotopically organized afferents from the skin. This

central nucleus is surrounded by a shell of neurons relaying afferents from joints and muscles. Rosén (1969) showed that in VB relay cells, activated by Group I afferents, IPSPs were evoked by cutaneous nerve stimulation. Therefore, VB relay cells transmitting kinesthesia are probably inhibited by cutaneous afferent impulses, as found in the somatosensory cortex by Mountcastle and Powell (1959).

On the basis of these various observations, it may be suggested that during the resting state of animals cutaneous sensory transmission in VB is given preference over kinesthetic transmission. When voluntary movements of limbs are initiated by PT impulses, preference of transmission in VB may shift from cutaneous sense to kinesthesia as a consequence of PT-induced facilitation of the joint-movement units and inhibition of the hair units. Thus, information about the precise position of the limbs is preferentially transmitted to SMC and may improve the control of voluntary movements. In other words, the role of the PT control system may change the functional state of VB relay cells so as to open the pathway for kinesthetic feedback information before the limbs are actually moved.

Towe (1973) cited a personal communication from Luschei and Clark that cutaneous sensibility was reduced about 60 msec prior to the first electromyographic response of voluntary contraction in a simple reaction time paradigm. This observation may support our suggestion that cutaneous sensory transmission in VB is suppressed via PT collaterals prior to movements of limbs.

Extraordinary Hair Units Receiving PT Excitation

In peripheral afferent fibers innervating hairs of the cat Brown and Iggo (1967) found three types of rapidly adapting units which innervated three kinds of hair follicle; down hairs, guard hairs and tylotrichs. They called these units Types D, G and T, respectively. Tylotrichs were the longest snd thickest hairs of the coat in the cat and Type T units were very sensitive to slight movements of the hairs (Straile, 1960; Brown and Iggo, 1967). Very recently Brown *et al.* (1974) reported ML units which responded to movements of tylotrichs. RFs of these ML units were very small, usually of only a few mm^2. Considering all these observations together, it seems possible that hairs represented by our extraordinary hair units may correspond to tylotrichs, although a definitive conclusion may be drawn only in future experiment aimed at identifying peripheral receptors.

The extraordinary hair units were excited by PT stimulation. In these units depression of excitability following ML stimulation is marked and long-lasting, while the depression following SMC stimulation is insignificant (Fig. 3D and E). This property is one of the characteristics of the joint-movement units (Tsumoto and Nakamura, 1974). In view of these facts, it is supposed that the extraordinary hair units may serve the control of movements as do the joint-movement units. These special units represent long hairs on the tips of the forepaw-digits or on the proximal end of the forearm. These hairs may be most easily stimulated when the animal moves his forelimb back and forth and touches objects. On that occasion information received by the extraordinary hair units of VB may play an important role in controlling movements of the forelimb.

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References

Andersen, P., Eccles, J.C., Sears, T.A.: The ventro-basal complex of the thalamus: Types of cells, their responses and their functional organization. J. Physiol. (Lond.) **174**, 370—399 (1964a)

Andersen, P., Eccles, J.C., Schmidt, R.F., Yokota, T.: Slow potential wave produced in the cuneate nucleus by cutaneous volleys and by cortical stimulation. J. Neurophysiol. **27**, 78—91 (1964b)

Andersen, P., Eccles, J.C., Schmidt, R.F., Yokota, T.: Identification of relay cells and interneurons in the cuneate nucleus. J. Neurophysiol. **27**, 1080—1095 (1964c)

Andersen, P., Junge, K., Sveen, O.: Cortico-fugal facilitation of thalamic transmission. Brain Behav. Evol. **6**, 170—184 (1972)

Andersson, S.A., Landgren, S., Wolsk, D.: The thalamic relay and cortical projection of Group I muscle afferents from the forelimb of the cat. J. Physiol. (Lond.) **183**, 576—591 (1966)

Brown, A.G., Iggo, A.: A quantitative study of cutaneous receptors and afferent fibers in the cat and rabbit. J. Physiol. (Lond.) **193**, 707—733 (1967)

Brown, A.G., Gordon, G., Kay, R.H.: A study of single axons in the cat's medial lemniscus. J. Physiol. (Lond.) **236**, 225—246 (1974)

Burchfiel, J.E., Duffy, F.H.: Corticofugal influence upon cat thalamic ventrobasal complex. Brain Res. **70**, 395—411 (1974)

Chambers, W.W., Liu, C.N., McCouch, G.P.: Inhibition of the dorsal column nuclei. Exp. Neurol. **7**, 12—23 (1963)

Creutzfeldt, O., Fuster, J.M., Herz, A., Straschill, M.: Some problems of the information transmission in the visual system. In: Eccles, J.C. (Ed.): Brain and Conscious Experience, pp. 138—164. Berlin-Heidelberg-New York: Springer 1966

Dawson, G.D.: The effects of cortical stimulation on transmission through the cuneate nucleus in the anesthetized rat. J. Physiol. (Lond.) **142**, 2—3 (1958)

Gordon, G., Jukes, M.G.M.: Descending influences on the extroceptive organization of the cat's gracile nucleus. J. Physiol. (Lond.) **173**, 291—319 (1964)

Iwama, K., Yamamoto, C.: Impulse transmission of thalamic somatosensory relay nuclei as modified by electrical stimulation of the cerebral cortex. Jap. J. Physiol. **11**, 169—182 (1961)

Jabbur, S.J., Towe, A.L.: Analysis of the antidromic cortical response following stimulation at the medullary pyramids. J. Physiol. (Lond.) **155**, 148—160 (1961a)

Jabbur, S.J., Towe, A.L.: Cortical excitation of neurons in dorsal column nuclei of cat, including an analysis of pathways. J. Neurophysiol. **24**, 499—509 (1961b)

Levitt, M., Carreras, M., Liu, C.N., Chambers, W.W.: Pyramidal and extrapyramidal modulation of somatosensory activity in gracile and cuneate nuclei. Arch. ital. Biol. **102**, 197—229 (1964)

Magni, F., Melzack, R., Moruzzi, G., Smith, C.J.: Direct pyramidal influences on the dorsal-column nuclei. Arch. ital. Biol. **97**, 357—377 (1959)

Mountcastle, V.B., Powell, T.P.S.: Central mechanisms subserving position sense and kinesthesis. Bull. Johns Hopk. Hosp. **105**, 173—200 (1959)

Ogden, T.E.: Cortical control of thalamic somato-sensory relay nuclei. Electroenceph. clin. Neurophysiol. **12**, 621—634 (1960)

Rosén, I.: Excitation of Group I activated thalamocortical relay neurons in the cat. J. Physiol. (Lond.) **205**, 237—255 (1969)

Shimazu, H., Yanagisawa, N., Garoutte, B.: Cortico-pyramidal influences on thalamic somatosensory transmission in the cat. Jap. J. Physiol. **15**, 101—124 (1965)

Straile, W.E.: Sensory hair follicles in mammalian skin. Amer. J. Anat. **106**, 133—147 (1960)

Takahashi, K.: Slow and fast groups of pyramidal tract cells and their respective membrane properties. J. Neurophysiol. **28**, 908—924 (1965)

Towe, A.L.: Somatosensory cortex: Descending influences on ascending systems. In: Handbook of sensory physiology, vol. II, pp. 701—718. Ed. by A. Iggo. Berlin-Heidelberg-New York: Springer 1973

Towe, A.L., Jabbur, S.J.: Cortical inhibition of neurons in dorsal column nuclei of cat. J. Neurophysiol. **24**, 488—498 (1961)

Tsumoto, T.: Characteristics of the thalamic ventrobasal relay neurons as a function of conduction velocities of medial lemniscal fibers. Exp. Brain Res. **21**, 211—224 (1974)
Tsumoto, T., Nakamura, S.: Inhibitory organization of the thalamic ventrobasal neurons with different peripheral representations. Exp. Brain Res. **21**, 195—210 (1974)
Wiesendanger, M.: The pyramidal tract. Recent investigations on its morphology and function. Ergebn. Physiol. **61**, 72—136 (1969)
Winter, D.L.: Nucleus gracilis of cat. Functional organization and corticofugal effects. J. Neurophysiol. **28**, 48—70 (1965)

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