

CONTRIBUTION OF POLYSYNAPTIC PATHWAYS TO THE TONIC VIBRATION REFLEX

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Summary 1) Unit discharges produced by either muscle vibration (the tonic vibration reflex, TVR) or electric stimulation of muscle nerve (the monosynaptic reflex, MSR) were recorded on the ventral root filament in the unanesthetized spinal or decerebrate preparation. The effect of tetanization of synergist and contralateral sural nerve was studied and the TVR was compared with the MSR under thiopental anesthesia. 2) Tetanization (250/sec, 10 sec) of synergist nerve produced potentiation of the TVR for a few minutes in both decerebrated and spinal preparations. 3) Tetanization of the contralateral sural nerve also potentiated the TVR in decerebrate preparations but not in the spinal preparations. 4) A small dose of thiopental sodium (2–10 mg/kg, *i.v.*) markedly suppressed the TVR, whereas production of the MSR was facilitated. 5) When the muscle was stimulated by repeated vibratory bursts, reflex discharges gradually increased as the trials were repeated in both decerebrate and spinal preparations. 6) On the basis of these facts, it was suggested that polysynaptic pathway through G1a activation, which was at least partly segmental, plays an important role in generating the TVR.

It has been well established that Group Ia afferent volleys evoke EPSPs monosynaptically on the motoneuron which innervates the same muscle from which the G1a fibers originate. However, several workers (ECCLES *et al.*, 1960; GRANIT, 1970; GRANIT *et al.*, 1957; TSUKAHARA and OHYE, 1964) have suggested that some polysynaptic pathways may participate in generating any type of tonic stretch reflex.

On the other hand, it has been observed in man, monkey (HOMMA *et al.*, 1971b), and cat (GILLIES *et al.*, 1971a; MATTHEWS, 1966) that vibration applied to the muscle tendon produced a tonic reflex contraction which was named “tonic vibration reflex” (TVR) (HAGBARTH and EKLUND, 1966a, b). It has been also

Received for publication December 29, 1971

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investigated that the TVR is powerfully influenced by various supraspinal structures and that it could not be produced in the spinal cat (GILLIES *et al.*, 1971a; MATTHEWS, 1966) or in patients who have a spinal lesion (DE GAIL *et al.*, 1966).

The characteristic slow development of tension and its high sensitivity to anesthesia suggested that the TVR was induced through several polysynaptic pathways (DE GAIL *et al.*, 1966; GRANIT, 1970; LANCE *et al.*, 1966). However, detailed mechanism of the generation of TVR is not yet clearly understood.

In the present study, an attempt was made to confirm, even if indirectly, that polysynaptic pathways have a certain role in the production of TVR in the cat.

METHODS

Experiments were performed on 20 cats decerebrated precollicularly under ether anesthesia. In 12 of the 20 cats the spinal cord was sectioned at the lower thoracic level (Th 10–11) during the experiment. Experiments were started at least 3 hr after decerebration. Some animals were immobilized with gallamine triethiodide and artificially ventilated. In most cases the left soleus muscle was used. The gastrocnemius muscle was also used occasionally. The left leg, hip, and tail were widely denervated by section and ligature except those leading to the lateral head of the gastrocnemius and soleus muscles. The gastrocnemius and soleus muscles were carefully separated from the surrounding tissues and each other in degrees appropriate to the vibratory experiment. A hook to which the tip of an electromagnetic vibrator was attached was inserted into the Achilles tendon. Laminectomy was performed from L4 to L7 and a smaller one at the lower thoracic level for spinalization.

Vibration of approximately 1 sec duration was applied to the soleus muscle once every 5 or 10 sec. Vibration frequencies used ranged between 40 and 200 Hz, with 100 Hz used in most cases. Ranges of the vibratory excursion were calibrated microscopically and were found to be within the range of 45 μ to 1.4 mm.

For the purpose of tetanization, the ipsilateral medial gastrocnemius nerve or the contralateral sural nerve was stimulated with 0.2-msec square wave pulses at 250/sec. Stimulus intensity was adjusted to 1.5–50 times the threshold for GI fibers, according to the experimental purpose. In order to compare the TVR with the monosynaptic reflex (MSR), the ipsilateral lateral gastrocnemius-soleus nerve was stimulated by a single electric shock (0.2-msec square wave pulse) during the inter-vibratory period. In this case the stimulus intensity was adjusted to the strength at which MSR, monitored as a single unit activity, sometimes failed to be elicited.

The TVR and the MSR were recorded as a single unit activity at the central cut end of L7 or S1 ventral root filaments. Identification of the gastrocnemius or soleus motoneurons was confirmed by their response to a brief manual stretching of each muscle.

Rectal temperature was maintained at 35–38°C. Blood pressure was monitored continuously through an intracarotic canula, and the blood pressure was maintained above 90 mm Hg by the intravenous infusion of physiological saline solution alone or a mixture of physiological saline solution and noradrenaline, if necessary.

The electromagnetic vibrator used was a Type G-10 (NAC Co., Ltd., Tokyo) which was driven by a function generator and AC power amplifier. A CdS photoconductive cell, which composed one arm of the Wheatstone bridge, was used to control both duration and unnecessary vibratory transients (WATANABE *et al.*, 1969). The time constant of amplitude modulation was 50 msec on the rising phase and 64 msec on the falling phase. The amplitude of vibration was monitored throughout all experiments.

RESULTS

1. *Effect of tetanization of synergist nerve and contralateral sural nerve on the TVR*

Post-tetanic potentiation was elicited by (1) tetanization of the muscle nerve which innervates the muscle tested, (2) tetanization of the crossed sural nerve, and (3) by pinna twist (GRANIT *et al.*, 1957). From these observations it was assumed that tonic stretch reflex, crossed extensor reflex, and pinna reflex had the common link of a certain polysynaptic chain. The present investigation was aimed at investigating the polysynaptic arc especially responsible for the TVR. The effect of tetanization of the synergist nerve, *i.e.*, medial gastrocnemius nerve, on the soleus motoneuron activity induced by vibration was studied on either decerebrate or lower spinal cats.

A fairly distinct potentiation was observed in 14 of 25 soleus motoneurons after tetanization of the central cut end of the medial gastrocnemius nerve. This potentiation effect was observed to be maintained for 1–3 min. For example, a motoneuron did not respond to the vibratory stimulation of 200 Hz (45 μ) in the control condition, as illustrated in Fig. 1. However, after tetanization it responded to the same vibratory stimulation with many spikes, and this augmentation lasted for about 80 sec. In 11 other motoneurons, however, such augmentation was not observed. Some of these unresponding motoneurons may belong to the phasic ones which were described by previous investigators (ANASTASIJEVIĆ *et al.*, 1968; GRANIT *et al.*, 1957).

The effect of tetanization was also tested in the lower spinal cat. The unitary reflex discharges induced by vibration were reduced to 70–80% of the control level by the spinal lesion, provided the ipsilateral ventral quadrant was saved intact. Complete spinal transection, however, markedly reduced these discharges. These observations correspond to those of MATTHEWS (1966), and GILLIES *et al.* (1971a). Of 13 motoneurons which responded to vibratory stimulation in the decerebrate state, 8 did not respond to the vibration after spinalization even if the amplitude

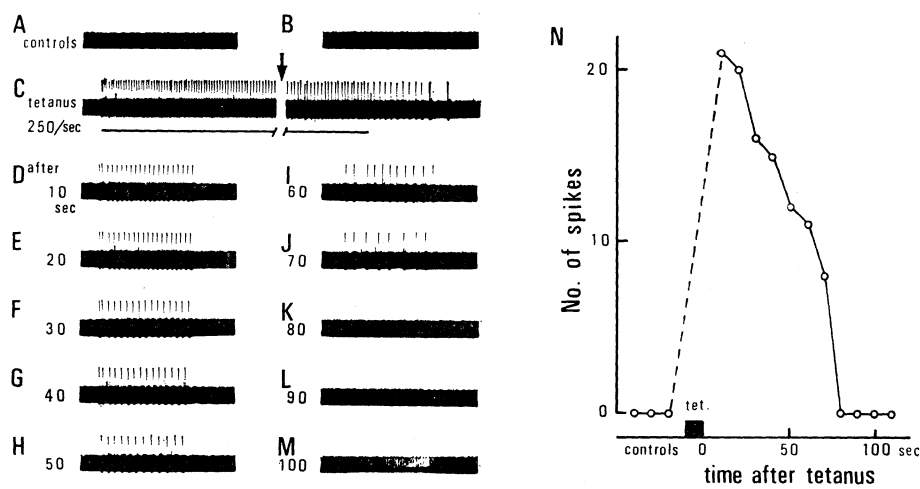


Fig. 1. Effect of tetanization of medial gastrocnemius nerve on the TVR in decerebrated cat. Activity of the soleus motoneuron was recorded at the isolated ventral root filament. Reflex response produced by vibration (200 Hz, 45 μ) before (A, B) and after (D-M) tetanization. The time after tetanization is indicated on the left side of each record. Two horizontal bars on the bottom indicate period of vibration of 1 sec duration. C shows response to tetanization by electric stimuli (0.2 msec, 250/sec, 10 sec) which is indicated by a horizontal bar just below the record. Record was omitted at arrow for about 7 sec. Partial records shown in A to M were plotted on the graph N. Ordinate represents number of spikes per vibratory stimulus. Abscissa represents the time after tetanization in seconds.

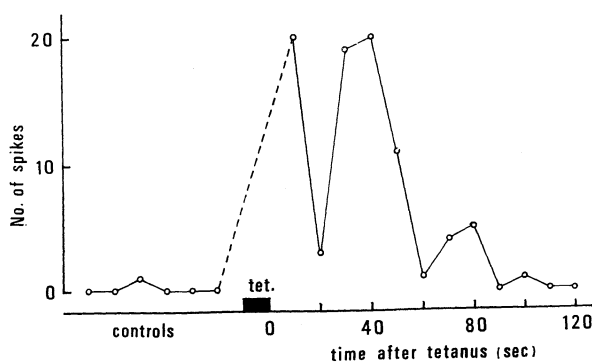


Fig. 2. Effect of tetanization of the medial gastrocnemius nerve on the TVR of the soleus motoneuron in a spinal cat. Plotting is the same way as in Fig. 1N except that the number in the ordinate represents the sum of the impulses obtained from 5 trials.

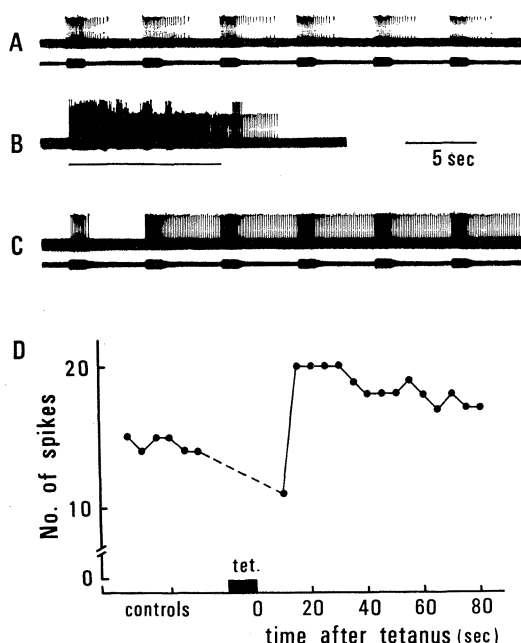


Fig. 3. Effect of tetanization of the contralateral sural nerve on the TVR in decerebrated cat. Response of soleus motoneuron to vibration (100 Hz, 200 μ) before (A) and after (C) tetanization. B shows response produced by tetanization (0.2 msec, 250/sec, $\times 30$). Duration is indicated by a thick horizontal bar. Results are plotted in D in the same way as the foregoing ones.

of vibration was fairly large. Five responded with only one or a few spikes during vibrations of 1 sec although the responses decreased markedly. In 7 of 13 motoneurons, the effect of tetanization was observed in the spinal state. The soleus motoneuron in Fig. 2 did not show any spike during vibration before tetanization. After tetanization of the medial gastrocnemius nerve reflex spikes were seen, although the number of spikes induced by each vibratory stimulus fluctuated considerably from one trial to another. It is obvious here that some potentiated state was attained and this condition lasted for about 2 min.

The effect of tetanization of the contralateral sural nerve on the TVR was tested. In decerebrated cat the potentiated state was also attained and lasted for a fairly long period, as shown in Fig. 3. This observation agrees with the results of GRANIT *et al.* (1957). However, this was not observed in the acute spinal cat.

2. Effect of thiopental sodium on TVR and MSR

It was pointed out that the MSR and the stretch reflex might even behave as if there were some competition (GRANIT, 1955). The stretch reflex tends, for in-

stance, to disappear in light anesthesia, whereas the monosynaptic response becomes even greater than before the administration of anesthetic. This paradoxical phenomenon was investigated in the present study with special attention to the relationship between the TVR and MSR, the latter being elicited by a single electric shock. In both cases unit discharges were recorded from the ventral root filaments. Vibratory stimuli of 1 sec duration were applied to the Achilles tendon of the soleus muscle once every 5 sec. An electric shock to the lateral gastrocnemius-soleus nerve was given during the inter-vibratory period, as shown in Fig. 4. Thiopental sodium (1% in distilled water) was injected intravenously during the recording of the TVR and MSR. The application of thiopental sodium (2–10 mg/kg) decreased the reflex discharge during the vibratory stimulus although elicitation of MSR by a single electric shock became more frequent, as can be seen in Fig. 4B. Further administration suppressed both the TVR and MSR, as shown in Fig. 4C. These results, partly shown in Fig. 4, are summarized in Table 1. Before the injection of thiopental sodium, the mean number of spikes elicited by

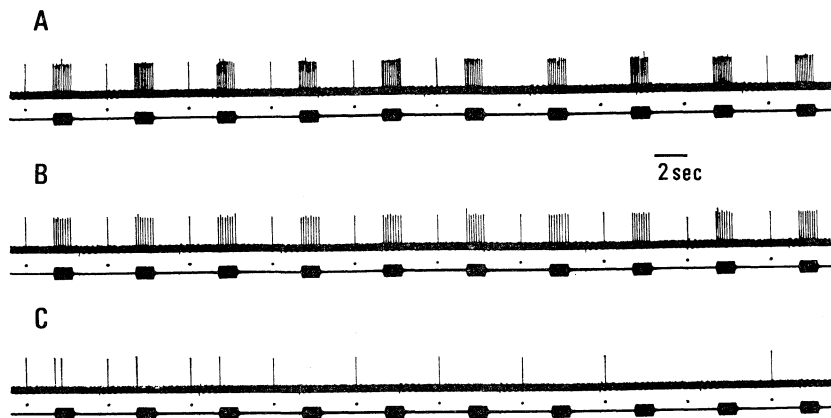


Fig. 4. Decerebrated cat. Responses of a soleus motoneuron produced by both vibration (100 Hz, 100 μ) and single electric shock given alternately (upper traces) and the monitored vibration (lower traces). Dots indicate the period of electric stimuli. A: Before application of thiopental sodium. B: After 10 mg/kg application. C: After 30 mg/kg application.

Table 1. The effect of thiopental sodium on TVR and MSR

	Percentage of elicitation of MSR	Number of spikes induced by 1 sec vibration
control	80.2%	10.6 ± 1.1 (N = 95)
thiopental sodium		
10 mg/kg	100	7.9 ± 0.8 (N = 32)
30 mg/kg	79.2	0.2 ± 0.4 (N = 24)

vibration of 1 sec duration was 10 ± 1.1 (S.D. of an observation), and the percentage of elicitation of MSR was 80.2%. After the injection, the former decreased to 7.9 ± 0.8 (S.D. of an observation), whereas the latter increased up to 100%. The difference in the number of spikes between before and after the administration is significant (t-test, $P < 0.01$). Administration of 30 mg/kg of the chemical still did not decrease the elicitation percentage of MSR in comparison with the control level, although TVR was almost completely suppressed.

3. Vibratory facilitation

As mentioned above, vibration applied to the muscle tendon produces a tonic reflex contraction of the muscle in man. The contraction has been known to be characterized by a very slowly developing tension (DE GAIL *et al.*, 1966; HAGBARTH and EKLUND, 1966a, b). The same reflex has also been observed in decerebrated cats or lightly anesthetized monkey (HOMMA *et al.*, 1971b). The time course of

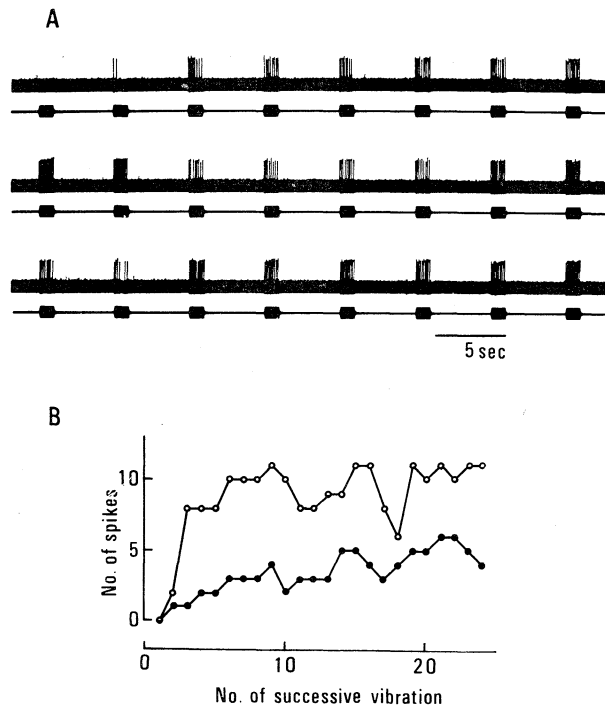


Fig. 5. Response of a gastrocnemius motoneuron to vibration. A: decerebrated cat. Upper trace; response to a series of interrupted vibratory stimuli of 80 Hz, 400 μ . Lower trace; monitored vibration. B: Number of spikes produced by each vibratory stimulus is plotted against the number of vibratory stimuli. Open circles: Results from a fiber in decerebrated cat. Solid circles: Results from the same fiber after spinalization. Vibratory amplitude in the spinal state was 800 μ . \circ , decerebrated state; \bullet , spinal state.

the development of tension, however, was quite different from that observed in man. Reflex tension of the cat reached its maximum value immediately after the onset of vibration and was then attenuated rather abruptly. This attenuation was either maintained as a plateau or gradually decreased. On the other hand, when vibration of 1 sec duration was repeated once every 5 or 10 sec the unitary reflex discharges on the ventral root filaments were gradually augmented as the vibration continued (HOMMA *et al.*, 1971a). In this series of experiments this phenomenon was also seen in 17 of 32 units. A typical example of this phenomenon is shown in Fig. 5A, which was obtained from a decerebrate preparation. The first vibration did not produce any reflex discharge. The second one, however, produced two spikes, and eight spikes were initiated by the third one. At the sixth vibratory stimulus the number of spikes reached the maximum value. These numbers are plotted in Fig. 5B (open circles). This facilitation was also observed in the spinalized state (Fig. 5B, solid circles). As shown here, this phenomenon was clearly seen even within the first several vibratory stimuli. In most cases the reflex discharge reached its maximum value at around the tenth vibratory stimulus. Appearance and time course of these phenomena were, however, strongly dependent on (1) the amplitude of vibration, (2) difference in motoneuron, and (3) the state of preparation.

DISCUSSION

It may be considered that the augmentation of the TVR observed after tetanization of the heteronymous synergist nerve is produced by an event at pre-motoneuronal level in the central nervous system, that is, PTP and/or a residue of tonic impulses from polysynaptic pathways. Since this phenomenon was observed in spinal preparation and its time course was very much like that of PTP (CURTIS and ECCLES, 1960; GRANIT, 1956; LLOYD, 1949; WILSON, 1956), it seems more likely that this is caused by PTP. Therefore, there has to be a common interneuron on these two excitatory pathways, one from the homonymous and the other from the heteronymous synergist muscle afferents to the same extensor motoneuron. This was observed in the following circumstance, when vibration amplitude was $45\ \mu$ and electric stimulation intensity was 1.5 times the lowest threshold of GI fiber, which is sufficient for the selective stimulation of the GIa alone or both GIa and GIb (BROWN *et al.*, 1967; ECCLES *et al.*, 1957). Therefore, muscle afferents consisting of this polysynaptic pathway may well include GIa fibers, at the least. Further systematic investigation is required to decide whether any other muscle afferents are concerned in the activation of this reflex arc or not. The assumption that polysynaptic pathways participate in generating the TVR is known to be supported by the following fact. The discrepancy between the effect of thiopental sodium on TVR and on MSR recorded on the functionally isolated ventral root filament seems to be difficult to explain if it is assumed that the TVR was induced

through the monosynaptic pathway alone. In the present investigation, the ventral root within the segments between L5 and S2 was completely severed. Therefore, it is unlikely that the decreasing effect of thiopental sodium observed was effected through the decreased vibratory sensitivity of the muscle spindle, which was mainly produced by reduced gamma activity. It is a well known fact that the polysynaptic chain is very sensitive to anesthesia. Therefore, it is considered here that the polysynaptic reflex arc plays a very important role in the generation of the TVR and that the decrease of the tonic discharge after thiopental injection is probably not due to depressed gamma activity but to suppressed interneuron activity, which plays some part in the activation of polysynaptic reflex pathway. With respect to this result, however, the difference between the effect of electrical and mechanical stimulation on motoneuron and the effect of thiopental sodium on the supraspinal center would require further examination.

The reason for the increased percentage of elicitation of MSR during the administration of thiopental sodium, as shown in Fig. 4 and Table 1, is not yet clear at the present stage of this study. The most probable explanation is the depression of the tonic presynaptic inhibition of the motoneuron, although ECCLES *et al.*, (1962) reported that pentobarbital increased the presynaptic inhibition. On the other hand, it has also been reported that vibration applied to the muscle suppressed the H-reflex (HAGBARTH and EKLUND, 1966a; YAMANAKA, 1964) and the tendon jerk (DE GAIL *et al.*, 1966). Recently it has been suggested that this inhibition is due to presynaptic inhibition (GILLIES *et al.*, 1969). Further investigation will be required to decide whether interneurons mediating the TVR are directly related with the activity which mediates presynaptic inhibition of motoneuron or not.

Vibratory facilitation can be clearly explained if we postulate a polysynaptic pathway which probably participates in generating the TVR. The fact that vibratory facilitation was also observed in the spinal preparations in which ventral roots between L5 and S2 were completely severed appears to be explained mainly by the phenomenon of the PTP or the temporal summation. TAKANO (1970) also reported that the reflex active tension became larger as the muscle received repetitive stretch, even though the spindle discharges did not show any alteration. In respect to the PTP, it is unlikely that 100 Hz vibration of 1 sec duration potentiated the monosynaptic G1a terminal, because it has already been reported that monosynaptic EPSP did not increase after such a short period of stimulation as above (CURTIS and ECCLES, 1960). On the other hand, many spinal interneurons respond with repetitive spike bursts to a single electric shock of the dorsal root filaments (FRANK and FUORTES, 1956). It is then very probable that the PTP was elicited at the axon terminal of these interneurons during 100 Hz vibration of 1 sec duration. All these present results seem to suggest that some polysynaptic pathways through G1a activation play an important role in generating the TVR. It is also suggested that these polysynaptic pathways are at least partly segmental.

It is well known that the descending tracts have a powerful influence on inter-

neurons mediating many segmental reflexes. It was reported that the vestibulo-spinal tract had excitatory action on the interneuron which mediates a crossed extensor reflex action and that this effect is exerted by monosynaptic action of the last order interneurons which have a direct synaptic contact with motoneurons (TEN BRUGGENCATE *et al.*, 1969). It was also observed in the present experiment that the TVR was facilitated after tetanization of the contralateral sural nerve. Furthermore, a recent study (GILLIES *et al.*, 1971a, b) suggested that the vestibulo-spinal tract was the most important bulbospinal pathway facilitating the TVR in the cat. On the basis of these facts it is suspected that the polysynaptic reflex arcs mediating the TVR and crossed extensor reflex and the vestibulo-spinal tract are linked with each other at the pre-motoneuronal level.

On the other hand, in our recent study (HOMMA *et al.*, 1971a) interspike intervals during TVR activity closely corresponded to the cyclic time of vibration up to around 200 Hz. Intracellular experiment has also shown that the rate of EPSPs corresponded with the vibration, although the upper limit of vibratory frequency used was fairly low (HOMMA *et al.*, 1970). Hence, it is possible to suggest that the firing of motoneuron during vibration may well show synchronous excitation with some of the summits of monosynaptic EPSPs which are superimposed on the interneuronal EPSPs.

The author expresses his gratitude to Professor S. Homma, Professor M. Kano, and Professor K. Takano for their valuable advice and criticism, and to Professor S. Watanabe for correction of the manuscript.

REFERENCES

- ANASTASIEVĆ, R., ANOJČIĆ, M., TODOROVIĆ, B. and VUČO, J. (1968) The differential reflex excitability of alpha motoneuron of decerebrate cats caused by vibration applied to the tendon. *Brain Res.*, **11**: 336-346.
- BROWN, M. C., ENGBERG, I., and MATTHEWS, P.B.C. (1967) The relative sensitivity to vibration of muscle receptors of the cat. *J. Physiol.*, **192**: 773-800.
- CURTIS, D. R. and ECCLES, J. C. (1960) Synaptic action during and after repetitive stimulation. *J. Physiol.*, **150**: 374-398.
- DE GAIL, P., LANCE, J. W., and NEILSON, P. D. (1966) Differential effects on tonic and phasic reflex mechanisms produced by vibration in man. *J. Neurol. Neurosurg. Psychiat.*, **29**: 1-11.
- ECCLES, J. C., ECCLES, R. M., and LUNDBERG, A. (1957) Synaptic actions on motoneurons in relation to the two components of the group I muscle afferent volley. *J. Physiol.*, **136**: 527-546.
- ECCLES, J. C., ECCLES, R. M., and LUNDBERG, A. (1960) Types of neurone in and around the intermediate nucleus of the lumbosacral cord. *J. Physiol.*, **154**: 89-114.
- ECCLES, J. C., SCHMIDT, R. F., and WILLIS, W. D. (1962) Presynaptic inhibition of the spinal monosynaptic pathway. *J. Physiol.*, **161**: 282-297.
- FRANK, K. and FUORTES, M. G. F. (1956) Unitary activity of spinal interneurons of cats. *J. Physiol.*, **131**: 424-435.
- GILLIES, J. D., BURKE, D. J., and LANCE, J. W. (1971a) Tonic vibration reflex in the cat. *J. Neurophysiol.*, **84**: 252-262.

- GILLIES, J. D., BURKE, D. J., and LANCE, J. W. (1971b) Supraspinal control of tonic vibration reflex. *J. Neurophysiol.*, **84**: 302-309.
- GILLIES, J. D., LANCE, J. W., NEILSON, P. D., and TASSINARI, C. A. (1969) Presynaptic inhibition of the monosynaptic reflex by vibration. *J. Physiol.*, **205**: 320-339.
- GRANIT, R. (1955) Receptors and Sensory Perception. Yale Univ. Press, New Haven, pp. 235-236.
- GRANIT, R. (1956) Reflex rebound by post-tetanic potentiation. Temporal summation-spasticity. *J. Physiol.*, **131**: 32-51.
- GRANIT, R. (1970) The Basis of Motor Control. Academic Press, London, pp. 103-109, 172-177.
- GRANIT, R., PHILLIPS, C. G., SKOGLUND, S., and STEG, G. (1957) Differentiation of tonic from phasic alpha ventral horn cells by stretch, pinna and crossed extensor reflexes. *J. Neurophysiol.*, **20**: 470-481.
- HAGBARTH, K.-E., and EKLUND, G. (1966a) Motor effects of vibratory muscle stimuli in man. In Muscular Afferents and Motor Control. Nobel Symposium I, ed. by Granit, R. Almqvist and Wiksell, Stockholm, pp. 177-186.
- HAGBARTH, K.-E. and EKLUND, G. (1966b) Tonic vibration reflex (TVR) in spasticity. *Brain Res.*, **2**: 201-213.
- HOMMA, S., ISHIKAWA, K., and STUART, D. G. (1970) Motoneuron responses to linearly rising muscle stretch. *Am. J. Phys. Med.*, **49**: 290-306.
- HOMMA, S., ISHIKAWA, K., and WATANABE, S. (1967) Optimal frequency of muscle vibration for motoneuron firing. *J. Chiba Med. Soc.*, **43**: 190-196.
- HOMMA, S., KANDA, K., and WATANABE, S. (1971a) Monosynaptic coding of group Ia afferent discharges during vibratory stimulation of muscle. *Jap. J. Physiol.*, **21**: 405-417.
- HOMMA, S., KANDA, K., and WATANABE, S. (1971b) Tonic vibration reflex in human and monkey subjects. *Jap. J. Physiol.*, **21**: 419-430.
- LANCE, J. W., DE GAIL, P., and NEILSON, P. D. (1966) Tonic and phasic spinal cord mechanisms in man. *J. Neurol. Neurosurg. Psychiat.*, **29**: 535-544.
- LLOYD, D. P. C. (1949) Post-tetanic potentiation of response in monosynaptic reflex pathway in the spinal cord. *J. Gen. Physiol.*, **33**: 147-170.
- MATTHEWS, P. B. C. (1966) The reflex excitation of the soleus muscle of the decerebrate cat caused by vibration to its tendon. *J. Physiol.*, **184**: 450-472.
- TAKANO, K. (1970) Reflexspannung und Gamma-Aktivität bei wiederholten Dehnungen von Extensormuskeln der Hinter-extremität decerebrierter Katzen. *Pflüg. Arch. ges. Physiol.*, **316**: 63.
- TEN BRUGGENCATE, G., BURKE, R., LUNDBERG, A., and UDO, M. (1969) Interaction between the vestibulospinal tract, contralateral flexor reflex afferents and Ia afferents. *Brain Res.*, **14**: 529-532.
- TSUKAHARA, N. and OHYE, C. (1964) Polysynaptic activation of extensor motoneurons from Group Ia fibers in the cat spinal cord. *Experientia*, **20**: 628-629.
- WATANABE, S., KOBAYASHI, H., and HOMMA, S. (1969) An application of photoconductive cell for controlling transients in muscle vibration. *J. Chiba Med. Soc.*, **45**: 358-361 (in Japanese).
- WILSON, V. J. (1956) Post-tetanic potentiation of polysynaptic reflexes of the spinal cord. *J. Gen. Physiol.*, **39**: 197-206.
- YAMANAKA, T. (1964) Effect of high frequency vibration on muscle spindle in the human body. *J. Chiba Med. Soc.*, **40**: 337-346 (in Japanese).