# NEUROPHYSIOLOGIC PROPERTIES OF THE SUPRATRIGEMINAL NUCLEUS

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BRIDGMAN and ELDRED<sup>1)</sup> reported that application of light pressure to a tenuissimus muscle surface of cat elicited an action potential in the dorsal root filament. KAWAMURA and TAKATA<sup>2)</sup> also established that in the cat the trigeminal motoneuron responded to topically applied pressure to the surface of the masseter muscle. This phenomenon has been confirmed to be attributed to a deformation of the muscle spindle in the masseter muscle.

The nucleus supratrigeminalis, which is located between the caudal extremity of the trigeminal mesencephalic nucleus and the trigeminal motor nucleus, was first identified by LORENTE DE NÓ<sup>3)</sup>. Following TORVIK's anatomical findings<sup>4)</sup> and JERGE's report<sup>5)</sup>, the supratrigeminal nucleus of the cat is about 3.5 mm deep from the medullar surface and just above the trigeminal motor nucleus. TORVIK<sup>4)</sup> reported that this nucleus was an aggregation of interneurons in the trigeminal motor reflex pathway.

Responses of the trigeminal motor nucleus to afferent impulses, evoked by mechanical deformation of a muscle spindle of the mandibular muscle, have been well analyzed<sup>2,6</sup>. However, functional interrelations between the supratrigeminal nucleus and the trigeminal motor nucleus have not been well studied yet, and functions of the supratrigeminal nucleus as an interneuron in the trigeminal motor reflex pathway are still in discussion.

The present study was designed to explore the neurophysiologic properties of the supratrigeminal nucleus in the cat.

## MATERIALS AND METHODS

Fifteen adult cats were used, these were decerebrate and decerebellate animals prepared under Nembutal anesthesia (30 mg/kg i.p.). The recording electrode was inserted vertically about 3.5 mm deep from the medullar surface just above the trigeminal motor nucleus.

The potential of the neuron in this region was recorded extracellularly or intracellularly by a glass capillary micropipette filled with 2M K-citrate which was stereo-

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taxically inserted into the pons. The resistance of the electrode was about 20 megohms. To measure the response pattern of the neuron, the masseter nerve was isolated from the masseter muscle and used for stimulation. Two Pt wire rings embedded in polyethylene tubing were used for stimulating the cut central end of the masseter nerve. The surrounding tissues around this stimulative sleeve electrode were insulated with a liquid paraffin pool. Light pressure  $(20 \text{ g/mm}^2-30 \text{ g/mm}^2)$  was applied vertically and directly to the exposed surface of the masseter or temporalis muscle by means of a small steel rod (about  $1 \text{ mm}^2$  at the round tip) connected to the strain gauge (force-displacement transducer).

### RESULTS

A spontaneous spike discharge was consistently recorded from the electrode inserted into the pons about 1 mm or less above the trigeminal motor nucleus. The neuron in this region responded to the afferent volley of the masseter nerve, and showed a typical response patterns of the interneuron. As shown in FIG. 1, as a sample of the intracellular record, the nerve cell showed spontaneous discharges with about 25 msec of a spike interval and this spike interval was decreased to about 10 msec by a single volley applied to the low-threshold fibers of the isolated afferent masseter nerve.



FIG. 1. Response of an interneuron in the supratrigeminal nucleus to afferent volley of the masseter nerve. Upper trace: Spontaneous discharge of the interneuron. Lower trace: Response of the interneuron. Afferent volley was given at the arrow.

As shown in FIG. 2, three different types of responses were clearly identified from this region when pressure was topically applied to the ipsilateral masseter or temporalis muscle. The cell of the first type, named "M-Cell", was activated by only light pressure applied to the restricted site of the masseter muscle, but did not respond to pressure to any sites of the temporalis muscle. The second type cell, the "T-Cell", contrary to the M-Cell, responded only to pressure applied to the temporalis muscle and not to the masseter muscle. The third type cell, the "M  $\cdot$  T-Cell", responded to pressure to both the masseter and temporalis muscles.



FIG. 2. Response patterns of three different cells in the supratrigeminal nucleus. M-cell means the cell which responds to pressure applied only to the masseter muscle. T-cell means the cell which responds to pressure only to the temporalis muscle.  $M \cdot T$ -cell means the cell which responds to pressure to the both muscles. C: Control, M: Response to pressure to the masseter muscle, T: Response to pressure to the temporalis muscle.

FIG. 3 is a detailed view of the response of the typical  $M \cdot T$ -Cell. The background activity of about 30 spikes/sec of this cell was increased to about 56 spikes/sec by 20 g pressure applied to the focus site of the masseter muscle or of the temporalis muscle. In this figure, the same magnitude of pressure (20 g) was applied to either the masseter or temporalis muscle during the



FIG. 3. Typical response pattern of  $M \cdot T$ -cell by deformation of either the masseter or temporalis muscle.  $M_1$ : Response to 20 g pressure applied to the focus site of the masseter muscle.  $M_2$ : Response to pressure applied at about 20 mm apart from the focus site of the masseter muscle.  $T_1$  is the case when pressure applied to the temporalis muscle, and  $T_2$  is the case when pressure applied to out of focus site of the temporalis muscle.

upward deflection of the lower trace, and M-1 was the response when the pressure was applied to the masseter, and T-1 was the case when the temporalis muscle was pressed. In both records, an off-effect (silent phase) also appeared immediately after removal of pressure to the muscle. The off-effect continued for about 200 msec and the activity of the cell gradually recovered to the level of the background activity. Conversely, when pressure was applied at about 20 mm apart from the focus site in the muscle, the activity of this cell was decreased as indicated in M-2 and T-2 in the figure, and the off-effect was recognized after removal of the pressure. The muscle sites, from which the activity of nerve cell was produced by pressure, were distributed within the area about 2 cm around the focus site on the line running along the muscle fiber. Furthermore, these nerve cells fired up to 500 cps following an increase of pressure applied to the muscle. In this case of the M · T-Cell, the ratio of the spike frequency between the background activity and response activity was nearly 1:2. The same ratio occurred in both cases when either the masseter or the temporalis muscle was pressed. Therefore, the firing ratio of this  $M \cdot T$ -Cell between the masseter muscle stimulation and temporalis stimulation was nearly 1:1, and this ratio was termed as the activity coefficient,  $A_k$ .

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Whereas, when pressure stimuli were applied to the foci in both the masseter and temporalis muscles at the same time, the M  $\cdot$  T-Cell represented the summated response. As shown in FIG. 4 as a sample record, the spike frequency of this M  $\cdot$  T-Cell was increased from 16 spikes/sec to 30 spikes/sec by 30 g pressure applied to the temporalis muscle as illustrated in T. When 30 g pressure was additionally applied to the masseter muscle, as shown in T+M, the spike frequency of this cell increased to 50 spikes/sec. After removal of the pressure applied to these muscles the off-effect (silent phase) appeared for about 500 msec, and activity of the cell gradually recovered to the background activity level of 16 spikes/sec. The A<sub>k</sub> of this M  $\cdot$  T-Cell was also counted as nearly 1.



Fig. 4. Summated response of the  $M \cdot T$ -cell by pressure application to both ipsilateral temporalis muscle (T) and masseter muscle (M).

Response patterns of the M-Cell and T-Cell were also identified by means of the above described analytical technique. The response of a M-Cell is represented in FIG. 5. This cell responded only to pressure applied to a site of focus in the masseter muscle, but did not respond at all to pressure applied to any parts of the temporalis muscle. At removal of pressure to the masseter muscle, silent phase was also recognized as the off-effect. The similar phenomenon occurred in the T-Cell, and the background activity of the T-Cell was only stimulated by Ia afferent impulses from the temporalis muscle. Therefore, these facts indicate that the M-Cell and T-Cell were synaptically connected solely with the Ia afferent fiber from either the masseter or the

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FIG. 5. Typical response of the M-cell. M: Typical response to light pressure applied to the focus site of the masseter muscle. T: No response to pressure applied to any sites of the temporalis muscle.

temporalis muscle.

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The effect of intravenous administration of Succinylcholine (Sch) of 1.0 mg/kg on the background activity of the above described nerve cells in the pons was examined. Succinylcholine is known as a stimulant to the muscle spindle<sup>6,7,8)</sup>. As shown in FIG. 6, the spontaneous discharges of the nerve cell completely disappeared after about 20 sec of Sch injection. After about 40 sec,



250 msec

FIG. 6. Effect of succinylcholine on the background activity of interneuron in the supratrigeminal nucleus. C: Control. Pressure was applied to the masseter muscle during downward deflection of the lower trace in C. Record in the right side is an effect of Sch injection. 1: Immediately after Sch injection, 2: After 20 sec, 3: After 80 sec, 4: After 5 min of Sch injection.

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the spontaneous discharges reappeared gradually and the discharges increased with a lapse of time. The spike frequency completely recovered to the control level after about 5 min. of Sch injection. In the figure, C is the control before Sch injection, and downward deflection of the lower trace in C indicates pressure application to the masseter muscle. In the right hand records of the figure, number 1 is immediately after Sch injection, 2 is after 20 sec, 3 is after 80 sec and 4 is after 5 min of Sch injection.

In the next step of this experiment, effect of pressure applied to the antagonistic muscle was investigated. As shown in FIG. 7, frequency of the background spike potential of the  $M \cdot T$ -Cell was increased to about twice the control when pressure was applied to the ipsilateral masseter muscle (FIG. 7A)



FIG. 7. Effect of stretch of the ipsilateral digastric muscle on the spike potential of the  $M \cdot T$ -cell. Background activities of the  $M \cdot T$ -cell were activated by either deformation of the masseter muscle (A) or that of the temporalis muscle (B). Under activation of the  $M \cdot T$ -cell, the digastric muscle was also stretched. C is control.



FIG. 8. No response of the M-cell to stretch of the ipsilateral digastric muscle. A: Response to pressure applied to the masseter muscle, B: No response to stretch of the digastric muscle.

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or temporalis muscle (FIG. 7B), but stretch of the ipsilateral digastric muscle (antagonistic muscle of the masseter) did not effect on the spike frequency of the  $M \cdot T$ -Cell at all, as indicated by an upward deflection of the mechanogram. The activity of the M-Cell was also not affected at all by stretch of the ipsilateral digastric muscle. The whole time course of response of the M-Cell was illustrated in FIG. 8 as a sample record. The record (A) shows a response of the M-Cell to pressure applied to the masseter muscle and in the lower record (B) no response is seen following the stretch of the digastric muscle. These facts suggest that there are no convergence of the Ia afferent from the antagonistic muscle in this nerve cell.

Distribution ratio of these M, T and M  $\cdot$  T-Cells in the pons was evaluated through the recording of fifty-eight cells. In FIG. 9, ordinate indicates the number of cells examined and abscissa is the activity coefficient (A<sub>k</sub>) of each cell. Marks T and M in abscissa indicate the neuron which responded to pressure applied either to only the temporalis muscle or to the masseter muscle respectively. The neuron which showed a response 2.5 times greater to pressure to the focus of the masseter muscle than that to the temporalis muscle under the same magnitude of pressure was illustrated as A<sub>k</sub>=2.5 in the right side in abscissa.



 $F_{IG}$ . 9. Distribution ratio of M, T and M  $\cdot$  T-cells in the supratrigeminal nucleus. Marks M and T indicate the neuron which respond to pressure applied either only to the masseter muscle or only to the temporalis muscle.

The relation between the activity coefficient and the number of neurons showed the typical Gaussian's distribution. Fifty-six cells out of 58 cells were identified as the  $M \cdot T$ -Cell which have the activity coefficient ranging from

1.0 to 2.5. Only one cell was identified as the M-Cell and also only one cell was recognized as the T-Cell.

#### DISCUSSION

Considering the recording site of the present experiment and the response pattern of these nerve cells in the pons, we may strongly assume that our records were obtained from the supratrigeminal nucleus. As already pointed out by TORVIK<sup>4)</sup>, the nucleus supratrigeminalis is assumed to be an aggregation of interneurons in the trigeminal motor reflex pathway.

In the present experiment, it was clearly identified that there were three different types of supratrigeminal interneurons receiving the Ia afferent impulses from the jaw closing muscles. These were the M-Cell, T-Cell and  $M \cdot T$ -Cell. Both the firing pattern of the neuron to the jaw muscle deformation and the acceleration of spike frequencies of these neurons by intravenous administration of Sch, strongly suggested that these interneurons were synaptically connected with the Group Ia fiber from the jaw closing muscles. Fifty-six cells out of the explored 58 cells in the supratrigeminal nucleus were  $M \cdot T$ -Cell.

Only two were identified as the M-Cell and T-Cell, respectively. The M · T-Cell is considered as the essential neurons receiving information from the Group Ia fibers from the jaw closing muscles. Among these M · T-Cells the neuron with  $A_k = 1$  is to be the fundamental neuron in the nucleus supratrigeminalis. These neurons in the supratrigeminal nucleus obtained in this experiment showed, at least, two characteristic features of the response pattern of the interneuron as indicated by ECCLES et al.<sup>9)</sup> and FRANK et al.<sup>10)</sup> in the spinal interneuron. The spinal interneuron has a character which is able to follow to a peripheral afferent stimulation of up to 1000 cps. The present explored neurons also had a background activity and they were able to respond with a high frequency of up to 500 cps when the muscle was strongly pressed. The maximum firing rate of the trigeminal motoneuron is about 50 cps as indicated in our previous paper<sup>11)</sup>. In addition, the explored neurons were not at all affected by Group Ia afferent volleys from the antagonistic muscle, although the trigeminal motoneuron showed an antagonistic inhibition. From such different responses, the interneuron explored in this experiment can distinctly be distinguished from the trigeminal motoneuron.

The interneuron which was explored in this study was assumed to be specific cells as similar as the type A cell in the spinal interneurons determined by ECCLES et al.<sup>9)</sup> The type A cell in the spinal interneurons is effectively activated by the Group Ia volley from the biceps-semitendinosus, but not other afferent volleys from other muscles or from the skin.

JERGE<sup>5)</sup> reported that units of the supratrigeminal nucleus were separated

into three fundamental groups. These were interneurons activated by pressure stimulation of the intraoral structures, and the interneurons which showed activated response and inhibited response to the jaw opening movements. EISENMAN et al.<sup>12)</sup> also reported that a small group of cells in the immediate surrounding of the trigeminal motor nucleus responded to opening and closing of the mouth. The neuron explored in the supratrigeminal nucleus in the present study presumably belong to the interneuron which is activated by the jaw opening movements. We also detected that some neurons, in the adjacent area to the above described neurons, fired by pressure stimulation of the gingiva or palate.

The physiological role of the supratrigeminal interneurons in the trigeminal motor reflex is a problem requiring further research. However, the present results strongly suggest an existence of the disynaptic reflex arc via the supratrigeminal nucleus, in addition to the monosynaptic arc, in the trigeminal motor reflex. Further, we may speculate that these interneurons of the supratrigeminal nucleus may participate to inhibit the activity of the trigeminal motoneuron innervating antagonistic muscles.

### SUMMARY

The neurons responding to the mandibular muscle deformation were explored in the supratrigeminal nucleus region above the trigeminal motor nucleus, and the response pattern of these neurons were analyzed.

1. All of the neurons in the supratrigeminal nucleus showed a background activity, and it means that steady impulses from the jaw muscles flow into this nucleus. Deformation of the muscle spindle of the jaw closing muscles activated these background activities.

2. In the supratrigeminal nucleus three different types of interneurons which responded to the Ia afferents from the jaw closing muscles were clearly identified. The first type of cell is the M-Cell which responded only to the mechanical deformation of the masseter muscle, the second is the T-Cell, which responded only to the temporalis muscle. The third cell is the M  $\cdot$  T-Cell which is the fundamental cells in the nucleus and responded to both the masseter and temporalis muscles.

3. The  $M \cdot T$ -Cell showed the summated response when the masseter and temporalis muscles were stimulated at the same time. These interneurons were not affected at all by afferent impulses from the antagonistic muscle. Fifty-six cells out of explored 58 cells in the nucleus were identified as the  $M \cdot T$ -Cell, and one M-Cell and one T-Cell were identified, respectively. The  $M \cdot T$ -Cell with the activity coefficient  $A_k = 1$  is the fundamental cells in this nucleus.

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