RESPONSES OF SINGLE NEURONS OF THE VESTIBULAR NUCLEI TO LATERAL TILT AND CALORIC STIMULATION IN CATS

IZURU MATSUOKA and MASANORI MORIMOTO

It is well-known that caloric stimulation is originally a clinical test of the vestibular function and a reliable diagnostic method for lesions of the vestibular system, however responses of the vestibular nuclei to caloric stimulation in the unanesthetized and anesthetized animals still remain to be clarified. In the present experiments, an attempt was made to determine the responses of unitary discharges in the vestibular nuclei, mainly in the Deiters' nucleus, to caloric stimulation and lateral tilt stimulation in the pentobarbital anesthetized and unanesthetized cats, and to establish the physiological significance of the commissural connection by recording the responses of the single neurons in the vestibular nuclei to caloric stimulation of the ipsilateral and contralateral labyrinths in cats.

MATERIAL AND METHODS

Experiments were performed on 55 adult cats of both sexes, weighing 3.0 to 4.5 kg. These were previously confirmed to be normal by a gross neurological examination. All surgery was performed under diethyl ether-oxygen anesthesia. The trachea, right femoral artery and vein were cannulated. Both the right and left tympanic bullae were exposed by longitudinal incision of both sides of the fronto-lateral cervical skin. After trepanation of the middle part of each bulla (about 5 mm in diameter), the mucous membrane of the middle ear cavity was removed and the tympanic membrane incised. One small concentric bipolar steel electrode was inserted through the round window according to the method of Fredrickson et al. and Matsuoka. Metal tubes, 3 mm in diameter were inserted into the holes of right and left bullae and fixed with dental cement.

Five ml of water at a temperature of 30°C (cold stimulation) and 44°C (warm stimulation) were infused through the metal tube, allowing irrigation through the tympanic bulla and middle ear cavity to the external meatus. The head of the animal was fixed on a stereotaxic instrument which had been devised by the Brain Research Institute, Niigata University School of Medicine, Japan.

The animal was then immobilized by transecting the spinal cord at the level of C₁ or C₂, and was maintained by artificial respiration. The recording was started at least 4 hr after the termination of the surgical procedures and ether inhalation. The stereotaxic instrument with the fixed animal was mounted on a movable goniometer allowing up to 30° inclination in a lateral direction. The recording microelectrode was a glass-insulated gold wire 15 to
20 $\mu$m in diameter and 0.75 to 1.0 M$\Omega$ in electrical resistance. The electrode was inserted into the Deiters' nucleus, using a micromanipulator. The sites of recording were confirmed histologically after termination of the experiments.

Spontaneous firing rate of each unit was recorded in the horizontal position for 2 min or more, and the instrument was tilted to the left i.e. with the recording side down, at a speed of 2°/sec. The firing rate was observed in a tilt of 30° from the horizontal position. When the firing rate reverted to the previous level, (usually a few min), the instrument was tilted 30° to the right, i.e. with the recording side up, at the same speed and held in that position for 2 min. Thereafter, caloric stimulation with both cold and warm water was applied to the same single neurons in the horizontal level following the method previously described.\textsuperscript{12,13,15}

RESULTS

Anesthetized animals

Anesthetized cats injected i.p. with 20 mg/kg of pentobarbital sodium were used. The effects of caloric stimulation by cold and warm water on the unitary discharges were observed in the same single neurons of the vestibular nuclei, mainly in Deiteres' nucleus. The recording from the neurons showed injury discharges as being excluded from the experiments. The spontaneous unitary discharges in the anesthetized animals were relatively low and irregular in frequency, 0.5-40/sec, and the mean firing rate of 139 neurons was 13.2±0.8/sec (Table 1). Caloric stimulation of the middle ear cavity exhibited the following three effects on the unitary discharges of the vestibular nucleus: increased, decreased, and refractory.

Increased type

Even in the same animal individual neurons responded to caloric stimulation with variation. As shown in Table 2, 10 of 32 vestibular neurons responded to both cold and warm stimulation with an increase in frequency of the unitary discharges. The time-course of the increase of the discharges recorded from the increased type of 10 neurons showed an increase

<table>
<thead>
<tr>
<th>Firing rate/sec</th>
<th>Anesthetized animals</th>
<th>Unanesthetized animals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of units (%)</td>
<td>No. of units (%)</td>
</tr>
<tr>
<td>0-5</td>
<td>35 (25.2%)</td>
<td>12 (2.4%)</td>
</tr>
<tr>
<td>5-10</td>
<td>34 (24.5%)</td>
<td>79 (15.5%)</td>
</tr>
<tr>
<td>10-15</td>
<td>21 (15.1%)</td>
<td>88 (17.3%)</td>
</tr>
<tr>
<td>15-20</td>
<td>21 (15.1%)</td>
<td>91 (17.8%)</td>
</tr>
<tr>
<td>20-25</td>
<td>11 (7.9%)</td>
<td>69 (13.5%)</td>
</tr>
<tr>
<td>25-30</td>
<td>4 (2.9%)</td>
<td>72 (14.1%)</td>
</tr>
<tr>
<td>30-35</td>
<td>7 (5.0%)</td>
<td>33 (6.5%)</td>
</tr>
<tr>
<td>35-40</td>
<td>6 (4.3%)</td>
<td>23 (4.5%)</td>
</tr>
<tr>
<td>over 40</td>
<td>43 (8.4%)</td>
<td></td>
</tr>
<tr>
<td>Total No. of units</td>
<td>139</td>
<td>510</td>
</tr>
<tr>
<td>Mean firing rate±S.E.</td>
<td>13.1±0.8/SEC</td>
<td>21.2±0.5/SEC</td>
</tr>
</tbody>
</table>

S.E.: Standard error

Equilibrium Res Suppl. 4
Table 2. Effects of caloric stimulation on unitary discharges in the vestibular nuclei of unanesthetized and pentobarbital-anesthetized cats.

<table>
<thead>
<tr>
<th>Type of units</th>
<th>Cold stim. (30°C, 5 ml)</th>
<th>Warm stim. (44°C, 5 ml)</th>
<th>Anesthetized animals No. of units</th>
<th>Unanesthetized animals No. of units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increased</td>
<td>Increase</td>
<td>Increase</td>
<td>10 (31.3%)</td>
<td>52 (22.4%)</td>
</tr>
<tr>
<td>Decreased</td>
<td>Decrease</td>
<td>Decrease</td>
<td>8 (25.0%)</td>
<td>28 (12.1%)</td>
</tr>
<tr>
<td>Reversed type-I</td>
<td>Decrease</td>
<td>Increase</td>
<td>57 (24.6%)</td>
<td></td>
</tr>
<tr>
<td>Reversed type-II</td>
<td>Increased</td>
<td>Decrease</td>
<td>86 (37.1%)</td>
<td></td>
</tr>
<tr>
<td>Refractory</td>
<td>No-change</td>
<td>No-change</td>
<td>14 (43.7%)</td>
<td>9 (3.8%)</td>
</tr>
</tbody>
</table>

32 232

discharge rate immediately after irrigation. Maximal increase was observed 20 to 30 sec after caloric stimulation and the effects continued for approx. 120 sec. This type of neuron showed a relatively higher frequency of spontaneous unitary discharge rate about 20/sec before caloric stimulation, however maximal increase in discharge frequency was 40–54/sec after caloric stimulation.

Decreased type

Eight out of the 32 neurons responded to both caloric stimulation with a decrease in frequency of the unitary discharges. The mean frequency of the spontaneous unitary discharges in this type of neuron was 13.7/sec before caloric stimulation. Immediately after irrigation with cold and warm water, unitary discharges began to decrease with a peak effect in 40 to 50 sec. Some of the neurons showed a temporary complete disappearance of the discharges, then recovered gradually to the previous level approx. 150 sec after caloric stimulation.

Refractory type

Fourteen out of the 32 neurons responded to either cold or warm stimulation. The mean firing rate in this type of neurons had an extremely low frequency of spontaneous discharges below 10/sec.

Unanesthetized animals

Spontaneous unitary discharges of the vestibular nuclei in the encephale isolé preparation of the unanesthetized cat ranged in frequency from 0.5 to 70/sec and the mean frequency of 510 neurons was 21.2 ± 0.5/sec (Table 1). Responses of unitary discharges to caloric stimulation were classified into the following 5 types: increased, decreased, reversed type-I, reversed type-II, and refractory types.

Increased type

Fifty-two out of the 232 vestibular neurons responded to both cold and warm stimulation with an increase in frequency of unitary discharges. This type of neuron showed a relatively lower frequency of spontaneous discharges before the application of caloric stimulation. Fig. 1 shows the time-course of the changes in frequency of discharges recorded from this type of 52 neuron after caloric stimulation. The increased discharges reached a peak effect 10 sec after irrigation, and thereafter, declined to the previous level within 180 sec. The
Fig. 1. Changes in firing rate of unitary discharges after caloric stimulation of the ipsilateral labyrinth:
Before: Spontaneous unitary discharge rate.
Irrigation: 30°C 5ml, 44°C, I: Standard error.

increase in frequency of unitary discharges was more prompt and longerlasting in the una-
esthetized animals than in the anesthetized ones.

Decreased type

Decrease in frequency of vestibular unitary discharges caused by both caloric stimu-
lation was observed in 28 out of the 232 neurons. This type of neuron showed a relatively
higher frequency of spontaneous discharges, 25.2/sec, before the application of caloric
stimulation. With complete ablation of the unitary discharges no animal responded to
stimulation. Maximal reduction was found 30 to 40 sec after caloric stimulation and re-
verted gradually to the previous level within 150 sec. The time-course of the responses of
discharges to both cold and warm stimulation in this type of neuron is summarized herein.

Reversed type-I

Fifty-seven out of the 232 neurons responded to cold stimulation with a decrease and to
warm stimulation with an increase in frequency of unitary discharges. As described above,
the reversal in quantative responses to either cold and warm stimulation was never observed
in the anesthetized animals. The mean frequency of spontaneous discharges in this type of
neuron was 16.8/sec before caloric stimulation. As shown in Fig. 1, cold stimulation produced
a slight and short-lasting increase of the discharge rate. Thereafter, the frequency of unitary
discharges was considerably reduced with the decrease recovering gradually to the previous
level within 150 sec. Warm stimulation increased the unitary discharges and a peak effect
was observed 30 to 40 sec after stimulation. Occasionally, increased frequency of the dis-
charges was reached in 80/sec. Increase of discharges or a result of warm stimulation con-
Eighty-six out of the 232 vestibular neurons responded to cold stimulation with an increase and to warm stimulation with a decrease in the frequency of unitary discharges. This type of neuron showing a reversed response was most frequently observed in the unanesthetized animals. Mean frequency of the spontaneous discharges was 18.4/sec before application of caloric stimulation. As shown in Fig. 1, unitary discharges began to increase immediately after cold stimulation and a peak effect was observed in 20 to 30 sec. The increased unitary discharge rate declined gradually to the previous level 180 sec after caloric stimulation. Warm stimulation of the same neurons gradually decreased unitary discharges to a peak effect in 30 to 60 sec and sometimes complete abolition was seen for a few sec, this effect lasting for approx. 180 sec (Fig. 2 and Table 2).

Refractory type

Only 9 out of the 232 vestibular neurons did not respond to either caloric stimulation in the unanesthetized animals. The mean frequency of spontaneous discharges before stimulation was approx. 10.0/sec.

Effects of pentobarbital sodium on unitary discharges of the vestibular nuclei in the encephale isole preparation

Equilibrium Res Suppl. 4
PHYSIOLOGY OF VESTIBULAR NEURONS

Contrasting results on the vestibular unitary discharges and responses to caloric stimulation in the anesthetized cats suggested that further observations of the effects of pentobarbital sodium in the encéphale isolé preparation were necessary. Reversed type-I and -II of neurons in the unanesthetized animals shifted to increased, decreased or refractory type after the administration of a small dose of pentobarbital sodium. Fig. 3 shows a typical effect of the anesthetics on unitary discharges of the vestibular nuclei. In this figure of the unanesthetized cat, cold stimulation produced an increase in frequency of the unitary discharges while warm stimulation resulted in a decrease. An i.v. injection of 5 mg/kg of pentobarbital sodium markedly decreased spontaneous unitary discharges recorded from the same neuron. 5 to 10 min after the injection, the decreased response to warm stimulation was completely abolished without affecting the increased response to cold stimulation.

**Effects of caloric stimulation of contralateral labyrinth on the unitary discharges of the vestibular nuclei**

The increased type of neurons identified by both cold and warm stimulation of the contralateral labyrinth was 21 out of the 88 neurons. In this type, the frequency of the spontaneous discharges before the application of caloric stimulation was slightly higher than that in others. The increased frequency reached a maximum 10 to 40 sec after stimulation, and thereafter, declined to the previous level within 210 sec.

The decreased type of neurons identified by both cold and warm stimulation of the contralateral stimulation was 13 out of the 88 neurons. Neurons which responded to both kinds of caloric stimulation of the contralateral labyrinth with a decrease in frequency, showed

Equilibrium Res Suppl. 4
slightly lower spontaneous discharges before stimulation. The decreased response lasted for a minimum of 180 sec and the discharge rate reverted to the previous level within 210 seconds. Thirty-five out of the 88 neurons responded to cold stimulation of the contralateral labyrinth with a decrease while warm stimulation revealed an increase in the frequency. Cold stimulation of the contralateral labyrinth produced a profound decrease in frequency of the unitary discharges within 20 sec and reduced firing for 150 sec. Warm stimulation elicited an immediate increase when discharge and the peak effect were observed 20 sec after the stimulation. Thereafter, the increased frequency declined gradually to the previous level within 210 sec. Fourteen out of the 88 neurons responded to cold stimulation of the contralateral labyrinth with an increase and to warm stimulation with a decrease in frequency. The discharge frequency began to increase immediately after cold stimulation of the contralateral labyrinth and continued for 120 seconds. With either cold or warm stimulation of the contralateral labyrinth only 5 out of the 88 neurons responded. Table 3 summarizes response of the vestibular neurons to ipsilateral caloric stimulation in correlation with the response to contralateral stimulation. Twenty-one out of the 34 vestibular neurons identified as “the reversed type-II” by ipsilateral stimulation showed the response of “reversed type-I” to contralateral stimulation. These 21 neurons responded in a “mirror image” manner to ipsilateral and contralateral stimulation, that is, cold ipsilateral and warm contralateral stimulation produced an increase in discharge; warm ipsilateral and cold contralateral stimulation caused a decrease, as shown in Fig. 4.

Table 3. Responses of the same neurons in the vestibular nuclei to caloric stimulation of the ipsilateral and contralateral labyrinths.

<table>
<thead>
<tr>
<th>Type of units</th>
<th>Ipsilateral stimulation</th>
<th>No. of units</th>
<th>Contralateral stimulation</th>
<th>No. of units</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cold stim. (30°C, 5 ml)</td>
<td>Warm stim. (44°C, 5 ml)</td>
<td>Cold stim. (30°C, 5 ml)</td>
<td>Warm stim. (44°C, 5 ml)</td>
</tr>
<tr>
<td>Increased</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>16 (18.2%)</td>
<td>6 (6.8%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>3 (3.4%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>7 (7.9%)</td>
</tr>
<tr>
<td>Decreased</td>
<td>↓</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>6 (6.8%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>2 (2.3%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>5 (5.7%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>3 (3.4%)</td>
</tr>
<tr>
<td>Reversed type-I</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>6 (6.8%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>2 (2.3%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>2 (2.3%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>7 (7.9%)</td>
</tr>
<tr>
<td>Reversed type-II</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>3 (3.4%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>6 (6.8%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑</td>
<td>21 (23.9%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓</td>
<td>4 (4.6%)</td>
</tr>
<tr>
<td>Refractory</td>
<td>→</td>
<td>→</td>
<td>5 (5.7%)</td>
<td>→</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>→</td>
<td>5 (5.7%)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>88</td>
<td>88</td>
</tr>
</tbody>
</table>

↑: Increased, ↓: Decreased, →: No change

Equilibrium Res Suppl. 4
PHYSIOLOGY OF VESTIBULAR NEURONS

<table>
<thead>
<tr>
<th>Ipsilateral stim.</th>
<th>Contralateral stim.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Before</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Ir. → Cold stim. 30°C, 5 min</strong></td>
<td><strong>Before</strong></td>
</tr>
<tr>
<td><strong>30 sec</strong></td>
<td><strong>Ir. → Cold stim. 30°C, 5 min</strong></td>
</tr>
<tr>
<td><strong>90 sec</strong></td>
<td><strong>30 sec</strong></td>
</tr>
<tr>
<td><strong>Ir. → Warm stim. 44°C, 5 ml</strong></td>
<td><strong>Ir. → Warm stim. 44°C, 5 ml</strong></td>
</tr>
<tr>
<td><strong>30 sec</strong></td>
<td><strong>30 sec</strong></td>
</tr>
<tr>
<td><strong>90 sec</strong></td>
<td><strong>90 sec</strong></td>
</tr>
</tbody>
</table>

Fig. 4. Effect of caloric stimulation of the ipsilateral and contralateral labyrinths on the same single neuron of vestibular nuclei in the encéphale isolé preparation. Each impulse shows 10 discharges.

3, 6, and 4 out of the 34 neurons responding to the ipsilateral caloric stimulation as the reversed type-II were of the increased type, decreased type and reversed type-I, respectively, regarding response to contralateral stimulation. Among the increased type group, regarding the decreased type of neurons responding to ipsilateral caloric stimulation, no reciprocal response in a “mirror image” manner was observed with ipsi and contralateral stimulation.

Responses of the vestibular neurons to lateral tilt

Response of unitary discharges of the vestibular nuclei to lateral tilt was classified into 5 groups: 1) increased type in which lateral tilt to either or both directions produced a significant increase in the firing rate, 2) decreased type in which lateral tilt to either or both directions produced a significant decrease in the firing rate, 3) the reversed type-I in which the firing rate increased with lateral tilt to the left and decreased with tilt to the right, 4) the reversed type-II in which the firing rate decreased with the lateral tilt to the left and increased to the opposite direction, and 5) the refractory type in which the firing rate did not change significantly by lateral tilt in either direction. As shown in Table 4, 10, 56, 4, 19, 4 out of the 93 vestibular neurons exhibited these types respectively. Among the increased type of neurons, 7 neurons showed an increase in frequency in response to lateral tilt to both directions and the other 3 neurons responded to one direction only with a significant decrease in the firing rate. Fig. 5 shows the time course of changes in mean firing rate of the unitary discharge recorded from the increased type of 7 neurons (A), the decreased type of 50 neurons (B), the reversed type-I of 4 neurons (C), and reversed type-II of 19 neurons, when the head of animal was tilted sideways at 30° and held in that position for 2 min. The increased type and the reversed type-II of the neurons showed a relatively lower frequency of spontaneous discharges before lateral tilt, while the decreased type and reversed type-I of the neurons exhibited a higher frequency in the horizontal position. In the increased type of neurons,

Equilibrium Res Suppl. 4
Table 4. Responses of same neurons of the vestibular nuclei to lateral tilt stimulation

<table>
<thead>
<tr>
<th>type of units</th>
<th>Left Tilt</th>
<th>Right Tilt</th>
<th>No. of units (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increased</td>
<td>Increase</td>
<td>Increase</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Increase</td>
<td>No change</td>
<td>2 (10.7%)</td>
</tr>
<tr>
<td></td>
<td>No change</td>
<td>Increase</td>
<td>1</td>
</tr>
<tr>
<td>Decreased</td>
<td>Decrease</td>
<td>Decrease</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>Decrease</td>
<td>No change</td>
<td>4 (60.2%)</td>
</tr>
<tr>
<td>Reversed type-I</td>
<td>Increase</td>
<td>Decrease</td>
<td>4 (4.2%)</td>
</tr>
<tr>
<td>Reversed type-II</td>
<td>Decrease</td>
<td>Increase</td>
<td>19 (20.4%)</td>
</tr>
<tr>
<td>Refractory</td>
<td>No change</td>
<td>No change</td>
<td>4 (4.2%)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>93</td>
</tr>
</tbody>
</table>

Fig. 5. Responses of unitary discharges of the vestibular nuclei to lateral tilt in both directions.

the firing rate increased progressively after the onset of lateral tilt in either direction and the increased discharges reached a peak effect in approx. 30 sec, 10 sec after achieving an inclination of 30° from the horizontal level. The mean frequency of discharges in the decreased type of the neurons began to decrease immediately after the onset of lateral tilt in either direction until reaching a maximal effect in 3 to 4/sec. The reversed type-I and -II of the neurons showed a transient increase in frequency after the onset of lateral tilt in either direction. Thereafter, the frequency of the discharge was reduced considerably following a
PHYSIOLOGY OF VESTIBULAR NEURONS

Table 5. Response of same neurons of the vestibular nuclei to caloric simulation and lateral tilt to the left.

<table>
<thead>
<tr>
<th>Type of units</th>
<th>Caloric Stim.</th>
<th>No. of units</th>
<th>Left Tilt</th>
<th>No. of units</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cold stim.</td>
<td>Warm stim.</td>
<td>Left Tilt</td>
<td>No. of units</td>
</tr>
<tr>
<td>Increased</td>
<td>Increase</td>
<td>Increase</td>
<td>Decrease</td>
<td>2</td>
</tr>
<tr>
<td>Decreased</td>
<td>Decrease</td>
<td>Decrease</td>
<td>Increase</td>
<td>3</td>
</tr>
<tr>
<td>Reversed</td>
<td>Decrease</td>
<td>Increase</td>
<td>Increase</td>
<td>5</td>
</tr>
<tr>
<td>type-I</td>
<td></td>
<td></td>
<td>Decrease</td>
<td>3</td>
</tr>
<tr>
<td>Reversed</td>
<td>Increase</td>
<td>Decrease</td>
<td>Increase</td>
<td>1</td>
</tr>
<tr>
<td>type-II</td>
<td></td>
<td></td>
<td>Decrease</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>No change</td>
<td>1</td>
</tr>
<tr>
<td>Refractory</td>
<td>No change</td>
<td>No change</td>
<td>Increase</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Decrease</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>31</td>
</tr>
</tbody>
</table>

lateral tilt in either direction.

**Responses of the vestibular neurons to caloric stimulation and lateral tilt**

As shown in Table 5, responses to both lateral tilt and caloric stimulation in the same neuron were recorded from 31 single neurons of the vestibular nuclei. Two neurons of the increased type showed an increase in frequency with both cold and warm stimulation and six neurons of the decreased type exhibited a decrease with both stimulations. Eight neurons of reversed type-I showed a decrease in frequency with cold stimulation and an increase with warm stimulation. Eleven neurons of the reversed type-II showed a reverse response to type-I. Four neurons of the refractory type did not respond to either caloric stimulation. The predominant pattern of responses was seen in the reversed type-II.

Eleven out of the thirteen neurons to which the firing rate had been increased with cold stimulation showed a significant decrease in frequency in response to a lateral tilt to the left. On the other hand, eight out of the fourteen neurons to which the firing rate had been decreased with the cold stimulation exhibited a significant increase in frequency of response to a lateral tilt to the left. The other six of the latter neurons responded to the same inclination with a decrease in frequency. Among the four neurons of refractory type to caloric stimulation, three neurons showed an increase while the other one showed a decrease in frequency in response to a lateral tilt to the left.

**DISCUSSION**

In the present experiments, spontaneous unitary discharges in the vestibular nuclei of the unanesthetized animals were significantly decreased after i.v. administration of 5 mg/kg pentobarbital sodium. The mutually reversed responses of unitary discharges of both caloric stimulations to one direction (cold responses) were changed by anesthetics. The reversed type of neurons which responded to cold stimulation with a decrease or increase and to warm stimulation with an increase or decrease in the frequency of the unitary discharges was ob-
served only in the unanesthetized animals. The abolishing effect of a small dose of thiobarbital in the unitary responses of the vestibular nuclei to galvanic stimulation administered through the contralateral round window membrane in decerebrated cats, lead DeVito to the assumption that the crossed fiber connection between the bilateral vestibular nuclei was a multisynaptic pathway.

Several investigators have reported that commisural fibers connect the vestibular nuclei directly or through reticular formation. Gernandt and Thulin have not, however, been able to detect evoked potentials of considerable amplitude in the contralateral reticular formation. On the other hand, Shimazu and Precht succeeded in recording evoked potentials in the ventral part of the contralateral vestibular nuclei caused by electrical stimulation of the vestibular nerve in unanesthetized cats.

Gernandt and Duensing and Shafer divided vestibular neurons into the following four types regarding responses of unitary discharges to horizontal angular acceleration in ipsilateral and contralateral turning: type-I, type-II, type-III, and type-IV. Type-I of the neurons showed an increase in frequency with ipsilateral turning and a decrease with a contralateral one, while type-II exhibited responses opposite to those of type-I. Type-III of the units showed an increase with turning in either direction, while type-IV of the neurons showed a decreased with turning in both directions. Shimazu and Precht, and Precht et al. have reported that 205, 90, 10, and 1 of 306 neurons responding to horizontal rotation show type-I, -II, -III, and -IV responses respectively. The increased type, decreased type, reversed type-I and reversed type-II in these studies are therefore regarded as corresponding to the above-described type-III, type-IV, type-II, and type-I, respectively.

In the present experiments, however, the increased and decreased type in response to caloric stimulation of the ipsilateral labyrinth showed a higher percentage than that of type-III and -IV in their sample, while reversed type-II neurons were recorded less frequently than type-I neurons in those experiments. The percentage of the increased, decreased and refractory types neurons regarding the response to caloric stimulation of the contralateral labyrinth was approx. the same as for the response to the ipsilateral caloric stimulation.

Regarding response of contralateral labyrinth to caloric stimulation, the percentage of reversed type-I neurons was higher while with ipsilateral stimulation the reversed type-II neurons were most frequently observed. Continuous observation of the same single neuron in the vestibular nuclei of the ipsilateral and contralateral labyrinths confirmed that in the majority of neurons the response to contralateral caloric stimulation occurred in a "mirror image" manner compared to the response of the ipsilateral stimulation. These reciprocal responses appeared to have a typical reaction concerning the function of the vestibular system to kinetic body movement. DeVito et al. showed that galvanic stimulation of the ipsilateral and contralateral labyrinth had a reciprocal effect on the majority of vestibular neurons when applied through the round window. Shimazu and Precht have reported that type-I neurons in the vestibular nuclei are inhibited by stimulation of the contralateral vestibular nerve in the hemilabyrinthectomized cats. Our findings coincide well with those

Equilibrium Res Suppl. 4
PHYSIOLOGY OF VESTIBULAR NEURONS

by DeVito et al. and Shimazu and Precht 1966 despite different methods of stimulation.

The peripheral vestibular organs include semicircular canals and otoliths. The receptor structures in the former organ are known to be activated by an angular acceleration in the vertical, transverse or anteroposterior axis and by caloric stimulation. On the other hand, receptors of the otolith organs are known to be activated by gravity, centrifugal force and linear acceleration. The utricular maculae in particular are organs of major importance in postural reflex. Observations of the thornback ray by Lowenstein & Roberts (1950) demonstrated that the receptors in the sensory endings of the otolith organs responded to lateral and fore-and-aft tilts. Since the various labyrinthine reflexes from the body trunk were excluded in the present encephale isolé preparations, the changes in the firing rate of the vestibular nuclei response to lateral tilt could be caused by afferent impulses from the receptor endings in the otoliths. Adrian (1943) and Peterson (1967) reported that many cells in the vestibular nuclei of anesthetized cats increased their firing rate when the ipsilateral side was tilted down and decreased their frequency when the contralateral side was tilted down. In the present experiments on unanesthetized cats, however, response of the vestibular units to lateral tilt was predominantly the decreased type (60.2%), in which the firing rate decreased in response to a lateral tilt to either direction. The reversed type-I of response which showed an increase in frequency when the side of recording was tilted down and a decrease when that side was tilted up was found in only 4 (4.3%) of 93 units analysed. The discrepancy between the mode of responses to lateral tilt in the anesthetized and unanesthetized animals suggests a central inhibitory mechanism in the vestibular nuclei of the latter preparations.

SUMMARY

The response of unitary discharges of the vestibular nuclei to caloric stimulation and lateral tilt was studied in the encephale isolé preparation of unanesthetized and pentobarbital anesthetized cats. The mean frequency of the spontaneous discharges in the vestibular nuclei was significantly higher in the unanesthetized cats than in the pentobarbital anesthetized ones. The responses of 32 vestibular neurons to both cold and warm stimulation in the pentobarbital anesthetized animals were classified into the following three types: the increased, in which the frequency of the unitary discharges was increased by both caloric stimulations, the decreased, in which the frequency was decreased by both caloric stimulations and the refractory in which the frequency did not change with either caloric stimulation. In the unanesthetized animals, the response of 232 vestibular neurons was classified into the following five types, increased, decreased, reversed type-I in which the frequency of the unitary discharges was decreased by cold stimulation and increased by warm stimulation, reversed type-II in which the frequency was increased by cold stimulation and decreased by warm stimulation, and the refractory type. The reversed type of the vestibular neurons was observed only in the unanesthetized animals. Responses of the lateral tilt of 93 vestibular neurons were classified into 5 types; increased, decreased, reversed type-I (increase in the unitary discharge rate with ipsilateral and decrease with contralateral tilt), reversed type-II.
I. MATSUOKA and M. MORIMOTO

(due to ipsilateral and increase with contralateral tilt), and refractory type. The
diminished type of neuron was the predominant pattern in the responses of the lateral tilt
(60.2%).

Two main types of neurons were localized in the vestibular nuclei: those increasing
the frequency in response to ipsilateral tilt selectively, and the other increasing the frequency
in response to caloric stimulation with cold water.

REFERENCES

1) ADRIAN, E.D.: Discharges from vestibular receptors in the cat. J. Physiol. 101: 398–407,
1943.
2) DEVITO, R.V., BRUSA, A. & ARDUINI, A.: Cerebellar and vestibular influences on Deitersian
3) DUENSSING, F. & SCHAFFER, K.P.: Die Aktivität einzelnar Neurone im Bereich der Vestibulari-
skere bei Horizontalbeschleunigungen unter besonderer Berücksichtigung des vestibulären
4) FREDICKSON, J.M., SCHWARZ, D., & KORNHUBER, H.H.: Convergence and interaction of
vestibular and deep somatic afferents upon neurons in the vestibular nuclei of the cat. Acta
5) GERNANDT, B.: Response of mammalian vestibular neurons to horizontal rotation and
6) GERNANDT, B.E.: Handbook of Physiology, Section 1. Neurophysiology, Edited by Field,
8) GRAY, L.P.: Some experimental evidence on the connections of the vestibular mechanism
9) LOWENSTEIN, O. & ROBERTS, T.D.M.: The equilibrium function of the otolith organs of the
10) MATANO, S., ZYO, K. & BAN, T.: Experimental studies on the medial longitudinal fasci-
11) MATSUOKA, I.: The responses of single neurons of the vestibular nuclei to caloric stimulation
12) MATSUOKA, I.: The responses of single neurons of the vestibular nuclei to caloric stimulation
of ipsilateral and contralateral labyrinth in the cat. Practica Otologica kyoto, 62: 589–598,
1969.
13) MATSUOKA, I.: Distribution of choline acetylase and cholinesterase and the action of
14) MATSUOKA, I., FUKUDA, N., TAKAORI, S. & MORIMOTO, M.: Responses of single neurons
of the vestibular nuclei to lateral tilt and caloric stimulation in the intact and hemilabyrinthec-
15) MORUZZI, G. & POMPEIANO, O.: Inhibitory mechanisms underlying the collapse of
16) OYA, T.: Experimental studies on the nystagmogenoses. Wakayama Igaku 12: 777–811,
1960.
17) PETERSON, B.W.: Effect of tilting on the activity of neurons in the vestibular nuclei of the
18) PRECHT, W., SHIMAZU, H. & MARKHAM, C.H.: A mechanism of central compensation of
PHYSIOLOGY OF VESTIBULAR NEURONS


(Received September 1, 1972)