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# Responses of Inferior Olive Neurons to Stimulation of Semicircular Canals. II. Vertical Semicircular Canalss

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**In the present study, the vestibularly evoked activity of inferior olive (IO) neurons was examined to investigate the vertical vestibular information transmitted through the vestibulo-olivo-cerebellar climbing fiber pathway. The extracellular recording was made in 74 neurons of the IO of cats, while animals were sinusoidally rotated. Most of vestibularly activated IO neurons responded to the vertical rotation (roll) test and were found in or near the $\beta$ subnuclei (IO$\beta$). The vestibular IO neurons were activated, when the animal was rotated to the side contralateral to the recording site. In contrast to the observation that the gain of responses of yaw sensitive cells (YSC) was not changed by the rotation frequency, that of the roll-sensitive cells (RSC) decreased as the rotation frequency was increased. Regardless of RSC or HSC, IO neurons showed the tendency of phase-lag in their responses. The alternating excitatory and inhibitory phases of responses of RSC were dependent on the direction of head orientation, the characterstics of which are the null response plane (NRP) and the optimal response plane (ORP). The analysis based on the NRP of RSC showed that vestibular inputs from the ipsilateral anterior semicircular canal induced the NRP of the RSC response at about 45 degree counterclockwise to the longitudinal axis of the animal, and that those inputs were distributed to RSC in the rostral part of IO$\beta$. On the other hand, those from the posterior semicircular canal were related with the NRP at about 45 degree clockwise and with the caudal part of the IO$\beta$. These results suggest that IO neurons receive and encode the vestibular information, the priority of which seems to be the vertical component of the body movement rather than the horizontal ones.**

**Key Words: Inferior olive, Roll-sensitive cells, Null response plane**

## INTRODUCTION

Early studies on the vestibular inputs to cerebellar Purkinje cells (Eccles et al, 1966; Precht & Llinas, 1969; Llinas & Precht, 1972; Ito, 1982) postulated the hypothesis that Purkinje cells do not receive afferent information through climbing fiber (CF) pathways arising from inferior olivary (IO) complex. Their hypothesis is based on the finding that the cerebellar field potential evoked by stimulation of the ipsilateral vestibular nerve are mainly of a mossy fiber (MF) type. They suggest that the CF afferents to the vestibulocerebellum might be activated via pathways other than the vestibular nerve or by means of special pattern of afferent activity which cannot be evoked by electrical activation of the vestibular nerve.

However, recently accumulated neuroanatomical data indicate that vestibular information is transmitted to cells in several subregions of IO. Horseradish peroxidase studies revealed that medial and descending vestibular nuclei (MVN, DVN) send a heavy ipsilateral projection to $\beta$ subnucleus (IO$\beta$) and dorsomedial cell column of IO (Saint-Cyr & Courville, 1979; Carleton & Carpenter, 1983; Gerritis et al, 1985; Carpenter, 1988). In addition, the nucleus prepositus hypoglossi, which receive heavy bilateral inputs from the vestibular nuclei, projects contralaterally to the dorsal cap of Kooy and ipsilaterally to the restricted regions of medial accessory olive just lateral to IO$\beta$ (McCrea & Baker, 1985; DeZeeuw et al, 1993; Balaban & Beryozkin, 1994). Vestibular activation of IO neurons was also reported in histologic studies using deoxyglucose or Fos as a marker for neuronal activity. Almost all of this kind of studies showed that neuronal activity is altered specifically in IO$\beta$, dc and dmcc following sinusoidal rotation (Dascanio et al, 1981), centripetal acceleration (Kaufmann et al, 1991; Kaufman et al, 1992) and unilateral labyrinthectomy (Kitahara et al, 1995; Cirelli et al, 1996).

Neurophysiological recording studies also reported that IO neurons responded to vestibular signals. The vestibularly evoked CF responses of Purkinje cells could be recorded in the uvula and nodulus of the cerebellum (Precht et al, 1976; Barmack & Shojaku, 1992). More direct evidences for the responsiveness of IO neurons to vestibu-

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**ABBREVIATIONS:** CF, climbing fiber; DVN, descending vestibular nuclei; IO, inferior olive; IO$\beta$, $\beta$ subnucleus of inferior olive; MF, mossy fiber; MVN, medial vestibular nuclei; NRP, null response plane; ORP, optimal response plane; RSC, roll-sensitive cells; YSC, yaw-sensitive cells.

larly-evoked signals were reported in single-cell recording studies made upon IO$\beta$ neurons (Robinson et al, 1988; Barmack et al, 1993). These studies showed that the activity of IO$\beta$ neurons are phasically modulated by natural vestibular stimulation (sinusoidal rotation). Although the vestibular inputs are known to reach to specific IO subnuclei, it still remains unclear which types of positional changes or which parts of peripheral vestibular apparatus evoke these signals. At the level of cerebellar nodulus, CF activity was evoked by horizontally sinusoidal stimulation (Precht et al, 1976). At the level of IO$\beta$ neurons, neuronal activity was modulated by horizontal rotation in cats (Robinson et al, 1988), vertical (roll) rotation in rabbits (Barmack et al, 1993) and static roll tilt in cats (Dascanio et al, 1981).

Our recent study on cats (Park et al, 2002) indicates that vestibular signals are transmitted into mainly IO$\beta$ subnuclei and that their responsiveness is inhibitory in nature and is more prominent to stimuli along the vertical plane. The present study was focused on the responses of IO neurons to vertical rotations, and was undertaken to investigate whether there are any differences in the response profiles and the anatomical locations of responding IO neurons between the anterior and the posterior semicircular canals.

## METHODS

### *Animal preparation*

Experiments were carried out with 23 adult male cats, weighing 2.5~3.5 kg. Animals were initially anesthetized with ketamine hydrochlordie (40 mg/kg, i.m.), and anesthesia was subsequently maintained with urethane (1 g/kg, i.p.). The left saphenous vein was cannulated for infusing fluid and drugs, a tracheostomy was performed to allow artificial respiration. During recording sessions, cats were paralyzed with periodic injections of pancuronium bromide (0.5 mg/hr) and artificial ventilation was employed to keep the end-tidal $CO_2$ concentration between 3.5~4.5%. Rectal temperature was monitored and maintained by an electrical homeothermic blanket at a range of 36.5~37.5°C.

In each animal, midline incision was made between vertex and the second cervical vertebra to remove the overlying scalp and muscles. To expose the foramen magnum wider, the lower part of the occipital bone was removed and adjacent cervical muscles were deflected. Animals were then placed in a stereotaxic fixing apparatus mounted on a sinusosidal rotator. To minimize its movement during rotation, the body of the animal was fixed with soft pads and elastic straps in a case aligned with the longitudinal axis. The posterior part of animals head was lifted upward, so that it formed an angle of about 25 degree from the horizontal plane. Following a fixative placing in a stereotaxic apparatus, dural flap was opened over the foramen magnum and the dorsal surface of the brain stem was exposed.

### *Stimulation and recording*

The rotating table was sinusoidally oscillated (0.01~0.5 Hz) about the vertical axis or about the longitudinal axis. During vestibular stimulation the vision of the cat was always occluded by covering its eyes with black blindfold.

To discriminate input sources between the anterior and the posterior semicircular canals, the angle of animals head about the vertical axis was changed step by step until a minimum in the vestibularly evoked neuronal activity was detected (null response plane, NRP). On either side of this NRP, the phase of vestibularly evoked neuronal activity was shifted with respect to the sinusoidal forcing function by 180°. In most of cases, this NRP was closely related with the anatomical orientation of a functional pair of vertical semicircular canals; either right anterior-left posterior semicircular canals or right posterior-left anterior semicircular canals.

About 90° from their NRPs, it was also possible to record a vestibularly-evoked neuronal activity with peak response magnitude and clear phase contrast (optimal response plane, ORP). In roll stimulation test, these responses on the ORP was selected for the measurement of the gain and the phase shift of the responses.

Extracellular single-unit recording was made with tungsten microelectrode (1~3 M$\Omega$). Recording electrodes were tilted 30° posterodorsal to anteroventral and advanced with an electrically-driven hydraulic micromanipulator towards IO just rostral to the obex. The signals from the electrode were amplified (band width 10~10 kHz) and were displayed on an oscilloscope. A window discriminator was used to discriminate the action potential of a single neuron. The output of the window was stored on a personal computer through A/D converting interface

### *Identification of recording sites*

At the completion of the recording of each unit, an electrolytic lesion was made by passing a DC current (10~20 $\mu$A) for 15 sec. Animals were sacrificed with overdose anesthetic. Following transcardiac perfusion with 10% formalin solution, the brain stem was removed from the skull and was submersed in the same solution for 24 hours, and neutral red staining was performed on frozen sections (50 $\mu$m thickness) in a frontal plane. Reconstruction of marking lesions was based on the stereotaxic atlas of the cat (Berman, 1968).

## RESULTS

We recorded responses of 74 neurons located in the caudal half of the inferior olive. Of those, 51 neurons were activated by vestibular stimulation. Most of IO cells showed irregular spontaneous activity less than 1 spike/sec and characteristic waveforms that multiple wavelets followed the action potential.

### *Responses to sinusoidal rotation*

Among 48 neurons activated by sinusoidal rotation, 28 cells responded specifically to the vertical (roll) stimulation, 4 cells to both vertical and horizontal (yaw) stimulation, and 3 cells to horizontal rotation only. The remaining 13 cells were activated by either roll (7 cells) or yaw (6 cells) test, although their responsiveness to the other mode or rotatory stimulation were not evaluated.

Typical vestibularly evoked responses of IO neurons are shown in Fig. 1. Most of IO neurons, regardless of roll-sensitive or yaw-sensitive, were activated when the animal was

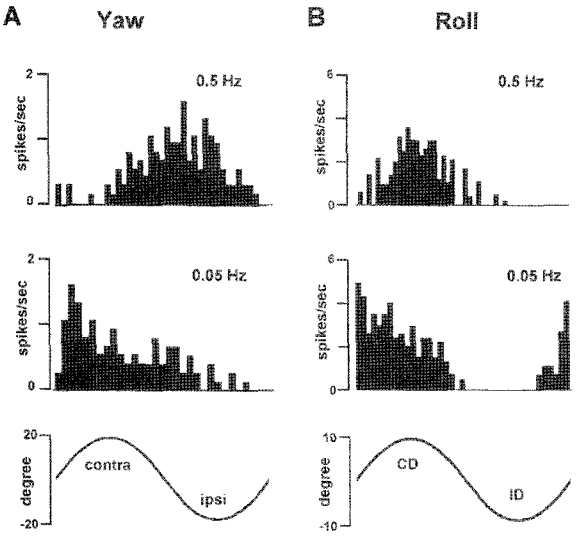


**Fig. 1.** Typical responses of yaw-sensitive (A) and roll-sensitive (B) neurons in the inferior olive. The response magnitude for yaw-sensitive neurons was tentatively smaller. Contra, towards contralateral side; ipsi, towards ipsilateral side; CD, contralateral side down; ID, ipsilateral side down.

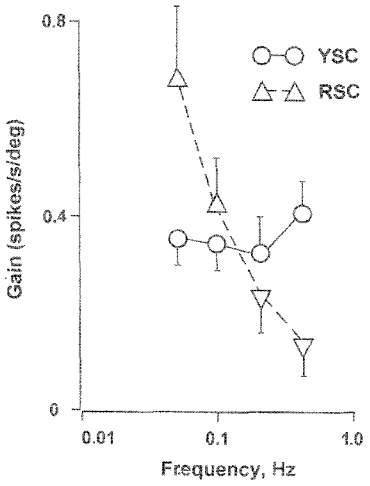


**Fig. 2.** Comparison of the gain of the response between roll-sensitive cells (RSC) and yaw-sensitive cell (YSC).

rotated to the side contralateral to the recording side, and were inhibited when the animal was rotated to the ipsilateral side. In most cases the response magnitude of yaw-sensitive cells (YSC) were smaller than that of roll-sensitive cells (RSC). Neuronal responses evoked by sinusoidal rotation revealed different excitation of an oscillation cycle, depending on the rotation frequency.

The assessment of the gain and the phase shift of neuronal responses showed a difference between RSC and YSC. As shown in Fig. 2 the gain of responses of YSC was not notably changed on different rotation frequencies. In contrast, the gain of responses of RSC apparently decreased as the rotation frequency increased.

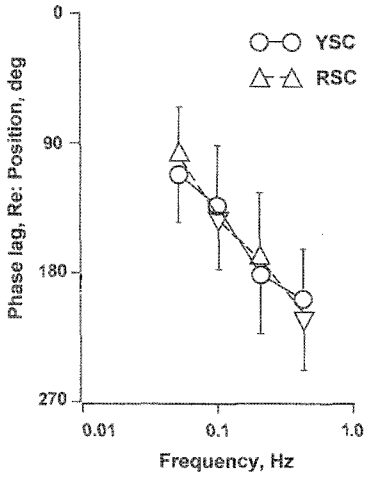


**Fig. 3.** Comparison of the phase lag of the response between roll-sensitive (RSC) and yaw-sensitive cells.

The phase of the response of each neuron to sinusoidal rotation shifted gradually in the pattern of phase-lag. In contrast with the case of the response gain, there was almost no difference between RSC and YSC in the degree of phase-lag on the certain rotation frequency (Fig. 3).

### *Optimal response plane and null response plane for roll-sensitive neurons*

The responses of roll-sensitive neurons were greatly influenced by the head position. The typical case representing this dependence of neuronal sensitivity on the head position is shown in Fig. 4. When the head position was aligned with a orientation of 46 degree clockwise with respect to the longitudinal axis (Fig. 4A), neuronal activity increased during the phase of right-side up (RU) and decreased during the phase of right-side down (RD). At this state, the evoked neuronal activity showed the rhythmical alteration of excitatory and inhibitory phases. However, in the head position of orienting 42 degree counterclockwise, this rhythmical alteration in the response disappeared and the over-all neuronal activity was decreased. (Fig. 4B). This head position was regarded as the null response plane (NRP).

When the head position was shifted slightly across the NRP to the 50 degree counterclockwise, the alteration of response phase reappeared (Fig. 4C). However, the response in Fig. 4C was 180 degrees out of phase in relation to the response in Fig. 4A. Although the response characteristics were similar between Fig. 4A and Fig. 4C except the response phase, the head position of Fig. 4A was selected as optimal response plane (ORP), on the basis that the ORP would be theoretically positioned at about 90 degrees of angle apart from the NRP.

### *Distribution of vertical vestibular information in IO*

The vertical vestibular information from two (anterior and posterior) semicircular canal seemed to be distributed to the different levels of IO (Fig. 3). In terms of ORP, neurons at the rostral level of IO responded to the rotation

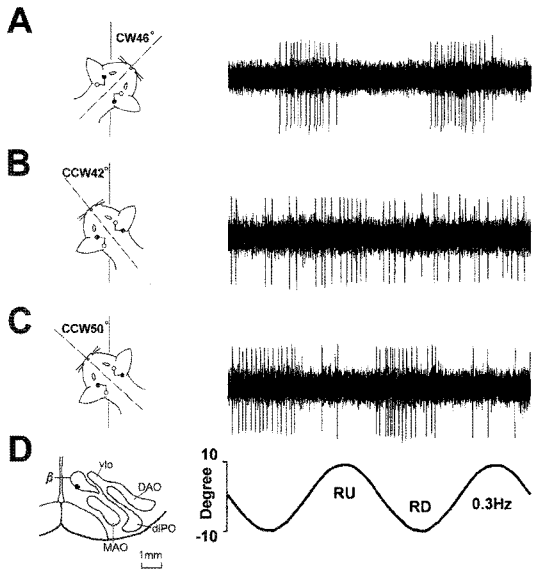


Fig. 4. The null response plane (NRP) and the optimal response plane (ORP) in the rostral IO. A, the response on the ORP. B, the response on the NRP. C, the altered neuronal reactivity 180 degrees out of phase in relation to the response in A on the plane slightly across the NRP. D, histological diagram illustrating the location of the recorded neuron. MAO, medial accessory olive; dlPO, dorsolateral principle olive; DAO, dorsal accessory olive; Vlo, ventrolateral out growth; CW, clockwise; CCW, counterclockwise; RU, right side up; RD, right side down.

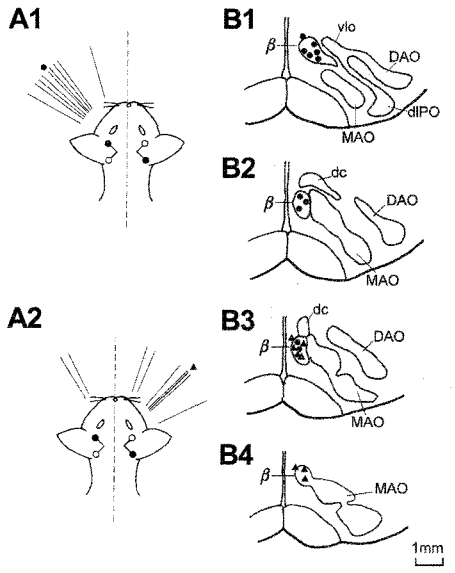


Fig. 5. Distribution of roll-sensitive neurons in IO for which the null response plane was identified. A1 and A2, null response planes for neurons in the rostral (B1 and B2) and the caudal (B3 and B4) part of the IO, respectively. dc, dorsal cap of Kooy. Other legends are as in Fig. 4.

with the head at the orientation of clockwise 45 degree. Neurons at the caudal level of IO showed their ORP at the head position of 135 degree clockwise (that is 45 degree counterclockwise). This finding implied that the input from the functional pair of ipsilateral posterior-contralateral anterior semicircular canals was transmitted to the rostral level of vestibular IO and that the input from the other functional pair (ipsilateral anterior-contralateral posterior) of the semicircular canals was transmitted to the caudal level of IO.

## DISCUSSION

In this study, most of vestibularly-driven IO neurons were activated in a phase that the head was rotated towards the contralateral side, which is consistent with previously reported data (Robinson et al, 1988; Barmack et al, 1993). This finding indicates that IO neurons were activated, while the contralateral semicircular canal was physiologically stimulated; the activation of the ipsilateral semicircular canal induced the inhibitory effect on the response of the vestibularly-sensitive IO neurons, suggesting that the vestibular projection fibers to IO neurons might have released an inhibitory neurotransmitter. It should be noted that in neurohistological studies vestibular inputs to IO have been reported to be mainly GABAergic inhibitory fibers (Nelson et al, 1989; Barmack et al, 1998). However, there still remain two unanswered questions regarding to the mechanism of inducing inhibitory and excitatory responses of IO neurons to vestibular inputs: 1) Does each IO neuron receive only the unilateral input? and 2) What is the influencing or modulating effect of cerebellar efferent fibers to IO on the responses of IO neuron?

The anatomical data (Walberg, 1974; Saint-Cyr & Courville, 1979; Gerritis et al, 1985) indicate that vestibular inputs arising from the medial and descending vestibular nucleus (MVN, DVN) project mainly unilaterally (ipsilaterally), and that another sources of vestibular inputs to IO, parasolitary nucleus, project to IO mainly ipsilaterally. According to these neuroanatomical data, the excitability of IO neurons should show only inhibitory responses such as the decreased spontaneous activities. Nonetheless, the response of IO neurons apparently revealed the excitatory phase (the increased neuronal firing rate), when the head was rotated to the contralateral side to the recording site. The simplest explanation for the activation of IO neurons is the excitatory inputs from vestibular receptors or nuclei in the contralateral side. However, as described below, so far there has been no neuroanatomical data to support this possibility.

Alternatively, the more reasonable explanation for the excitatory phase could be the concept of disinhibition. According to this assumption, the inhibitory driving effect of vestibular inputs to IO may cease, when the head is rotated to the contralateral side, which results in disinhibiting IO neurons and increasing the firing rate of IO neurons. However, on close scrutiny of this hypothesis, it is very clear that another inputs to IO, which play a role of disinhibiting IO neurons, is essential. Concerning the next question of where is the source of this disinhibitory inputs to IO, the most plausible condidate for this disinhibitory fibers might be cerebellar efferent fibers to IO. The inhibitory influence of the cerebellum on the excitability of IO neurons has been described in many other aspects of CF responses (Andersson et al, 1988; Ruigrok & Voogd, 1995).

The present study employed the technique of null response plane (NRP). It was regarded as the first step of

handling data to systemically identify the NRP and ORP. Different from vestibular inputs from horizontal canals, those from vertical canals were found to transmit more quantity and quality of vestibular information. Most of IO neurons responding to vertical vestibular stimulation were very sensitive to vector forcing direction, dependent on the head position. Therefore, in the analysis of data acquired from the vertical vestibular stimulation, only responses on the ORP were compared. The ORP and NRP represent their close relationship with the anatomical arrangement of semicircuflar canals in the head. Once again explaining the ORP and NRP in Fig. 4 in the anatomical aspect of semicircular canals, the ORP in Fig. 4A is coincided with the head position in which the functional pair of left posterior-right anterior semicircular canals (drawn as open circles) are placed in the most sensitive condition to rolling vector force. Alternatively, the NRP in Fig. 4B is coincided with the head position in which this functional pair or semicircular canals are placed in the least sensitive condition. The ORP and NRP were quite useful tools to identify from whose vertical canals the vestibular inputs to IO arise.

The finding that the number of specific RSC was much more than that of YSC suggested that IO neurons receive and encode the vestibular information with priority for the vertical component rather than the horizontal one. Anatomically, IO neurons receive the vestibular information not directly from peripheral vestibular receptors through the primary afferents, but indirectly from MVN, DVN or parasolitary nucleus through the secondary or tertiary fibers (McCrea et al, 2001). Therefore, the vestibular information transmitted to IO neurons would be rather the second-step information which was already at least partially integrated in the vestibular nuclei.

Actually, the co-sensitiveness to both horizontal and vertical canals, and features of decreasing gain and the phase lag tendency of responses of RSC observed in the present study suggested that vestibular responses of IO neurons are resulted from the combined inputs from semicircular canals and otolithic organs. Considering another aspect of the neural pathway transmitting the vestibular information to the cerebellum, CF pathway does not have to separately transmit receptor-specific information, which can be transmitted through MF pathway to Purkinje cells in the cerebellum (Voogd et al, 1996). Therefore, the less sensitivity of IO neurons to yaw stimulation does not imply that less fibers are projected from the horizontal canal to IO, but that the quantity or quality of vestibular information arising from horizontal canals may be less or low, respectively, compared to those from vertical canals. The present study showed that many aspects of responses of RSC are more adequate or concrete than those of YSC. For examples, the decreasing gain of RSC response could reflect the rotation frequency, and dependency of the phase shift in their responses on the head position could reflect the move of definitive direction (plane) of vertical rotation. These findings suggest that the amount of vestibular information transmitted to and handled in IO neurons are more focused on vertical components of the head movement than on horizontal ones.

It is well known that sensory inputs are somatotopically distributed within IO (See reviews of Kooy, 1916 and Azizi, 1989). Even in the optokinetic information, another kind of sensory modality related with the body movement, this somatotopic characterstic is established. Neurons responding to optokinetic stimulation in the horizontal plane appear to be located in the dorsal cap, and those responding in vertical planes are located more rostrally, closer to the ventrolateral outgrowth (Leonard et al, 1988). For the vestibular IO region, anatomical or physiological data accumulated up to date confirm that vestibularly-activated neurons are most abundant in IO$\beta$, which is mainly related with the vertical vestibular information. Any other subregions of IO complex have not been introduced as a vestibular IO specific for the horizontal vestibular information. It is possible that the horizontal components of the head movement might be encoded with or supported by other sensory modality, such as a vision or collic inputs in IO neurons (Maekawa & Simpson, 1973; Takeda et al, 1980; Gellman et al, 1985). Anyway, the present study showed that the somatotopic characteristic in vestibular IO could be accepted between anterior and posterior semicircular canals. Identified on the basis of their NRP and ORP, RSC related with the functional pair of ipsilateral anterior-contralateral posterior semicircular canals were found in the relatively rostral area of IO, whereas those related with the other functional pair were located in the caudal part of IO. These findings suggest that the major part of vestibular information encoded within vestibular IO are related with the vertical head movement.

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