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CANAL AND OTOLITH INPUTS TO SINGLE VESTIBULAR NEURONS IN CATS

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INTRODUCTION

Semicircular canals mainly sense angular accelerations, whereas otolith organs mainly sense linear accelerations. The saccular macula mainly sense vertical, and the utricular macula sense mainly horizontal, linear acceleration and tilt of the head, respectively. Both the receptors usually respond together during natural movements. The vestibulo-ocular and the vestibulospinal reflexes evoked by the semicircular canals and the otolith organs help to stabilize the visual image on the retina, and to restore the head position in space during movements, respectively.

It was observed that some vestibular relay neurons receive inputs from some of semicircular canals and otolith organs but others do not, when natural stimuli were applied in alert cats (1, 3, 18, 23, 24, 30, 53). By following the electrical stimulation of individual nerve branches of the vertical semicircular canals and otolitic nerves, synaptic potentials were recorded in the target vestibular nucleus neurons (6, 7, 14, 15, 17, 34, 36,~39, 41~44, 47, 49, 51), extraocular motoneurons, (4, 8, 9, 13, 15, 27, 40, 45, 50) and neck motoneurons (2, 10, 14, 15, 32, 35, 46, 48, 52). Syaptic potentials evoked in target interneurons after stimulation of some canal and otolith nerves had the same latecy range and axonal pathway (see Discussion), it is possible that some interneurons in the vestibular nuclei send information from different receptors (ampulla and macula) in the labyrinth to extraocular and neck motoneurons. In this paper, we studied the convergence of the posterior semicircular canal (PC) and saccular inputs, and of the PC and utricular inputs on single vestibular neurons, which were categorized according to their innervating targets. Vestibular nucleus neurons were classiffied as VO neurons (Vestibulo-Ocular proper neurons), VOS (Vestibulo-Oculo-Spinal neurons sending axon collaterals both to the extraocular motoneuron pools and to the spinal cord), VS neurons (Vestibulospinal proper neurons) and V neurons (vestibular nucleus neurons without axons either to the oculomotor nuclei or the spinal cord) on the basis of whether or not they responded antidromically to stimulation of the oculomotor nuclei and the spinal cord (16, 41-44). Some of the findings have been reported in an abstract and a proceeding on international symposium (54, 55).

METHODS

Experiments were performed on 28 cats in conformity with the "Guiding Principles for the Care and Use of Animals in the Field of Physiological Sciences; The Physiological Society of Japan, 1 988". Each cat was initially anesthetized with Ketamine hydrochloride followed by halothane and nitrous oxide inhalation. The cat was then decerebrated at the interfollicular level. Temporal and occipital craniotomy and laminectomies were performed. The caudal part of the cerebellum was aspirated to expose the floor of the fourth ventricle. Rectal temperature was maintained at 37.5°C. Blood pressure was monitored and maintained above 100 mmHg by intravenous infusion of 5-10% glucose solution. The animal was paralyzed with pancuronium bromide, and artificially ventilated.

In order to test for convergence of the saccular and PC nerves, or the utricular and PC nerves on single neurons in the vestibular nuclei, pairs of fine silver electrodes (acupuncture needles), that were insulated except for 0.25 ~ 0.5 mm at the tip, were placed into individual nerves in the left inner ear. The other vestibular nerve branches not to be stimulated were transected in the inner ear (27, 40, 48). The inter-electrode distance was approximately 0.8 mm. The inner ear was drained of liquid using a small piece of twisted cotton, and the electrodes were fixed to the occipital bone. To prevent the spread of stimulus current, these nerves and electrodes were covered with a warm semisolid paraffin-Vaseline mixture. Cathodal or anodal current pulses of 150~200 ms duration were applied to the saccular, utricular and PC nerves at a rate of 2-3 Hz. Monopolar tungsten electrodes were inserted into the caudal end of the oculomotor nuclei, and medial (M) and lateral (L) vestibulospinal tract (VST) at the C1 segment. The same monopolar electrodes were inserted into the bilateral C8 ~ Th1 and L3 segments (26). The animal was suspended by hip pins and a clamp on the T1 vertebra.

Field potentials were recorded from the vestibular nuclei with glass micropipettes containing 2 M NaCl saturated with Fast Green dye. The threshold for stimulation of the saccular, utricular and PC nerves to evoke N1 field potentials, which are due to monosynaptic activation of secondary vestibular neurons (25, 31) ranged from 5 to 45 mA. The threshold was comparable with those reported in previous papers (40, 45, 48, 49). Intracellular recordings were performed mainly from lateral and descending vestibular nucleus neurons using micropipettes filled with 2 M K citrate, with a resistance of 3-10 MW. Synaptic potentials were recorded following stimulation of the PC and either saccular or utricular nerve. Antidromic activation was also tested after stimulation of the oculomotor nuclei and spinal cord to determine innervating targets of the neuron.

RESULTS

We studied the convergence of both afferents of the PC nerve and saccular nerve, and that of the PC nerve and utricular nerve on single vestibular neurons. More than 200 vestibular neurons were classified as VO, VOS, VS and V neurons. To determine inputs to single vestibular neurons, the PC, saccular and utricular nerves were stimulated at an intensity of approximately 0.5-5 times the threshold of the N1 potential. These stimulus intensities were confirmed to be below the intensity of current spread to the other vestibular nerve branches (40, 45, 46, 49). Excitatory postsynaptic potentials (EPSPs), with latencies of 1.4 msec after stimulation of individual nerves, were of a monosynaptic nature (17, 22, 25, 28, 29, 31, 40). All but one of the inhibitory (I) PSPs in the VO, VOS, VS and V neurons were of a disynaptic nature (1.5 msec) in response to stimulation of individual nerves (17, 25, 28, 29, 31, 40, 45, 48, 49).

VO neurons

We studied 14 VO neurons after stimulation of the PC and saccular nerves and 4 VO neurons after stimulation of the PC and utricular nerves. All VO neurons responded to stimulation of either the PC alone or both the PC and otolith nerves. No VO neurons activated solely by stimulation of the saccular or utricular nerve were found (Fig. 1). Saccular and utricular nerve stimulation evoked monosynaptic and polysynaptic EPSP-IPSP sequences in five VO neurons which received PC inputs.

VOS neurons

In a series using PC and saccular nerve stimulation, we studied the input convergence on 14 VOS neurons. Convergence of the PC and utricular afferents were tested on 19 VOS neurons. Only two VOS neurons without inputs from the PC produced polysynaptic IPSPs following stimulation of either the saccular or the utricular nerves (Fig. 1). On the other hand, PC-activated VOS neurons without otolith inputs made up 55% (18/33), almost all of which received monosynaptic EPSPs after stimulation of the PC nerve. Convergence of PC and otolith afferents was seen in 13 (39%)neurons (Fig. 1). About one quarter of the convergent neurons were activated monosynaptically after stimulation of both the PC and otolith nerves. The remaining convergent neurons received monosynaptic inputs from the PC nerve and polysynaptic EPSP-IPSP sequences in response to stimulation of the otolith nerves, or vice versa. Most of the VOS neurons were activated antidromically from the electrode inserted into the MVST.

VS neurons

A hundred and four VS neurons were studied. As shown in Figure 1, considerably more (41) VS neurons with convergent inputs were found than neurons sending axons to the oculomotor nuclei (VO and VOS). About three quarters (29/41) of convergent VS neurons in both groups were activated monosynaptically following stimulation of the PC nerve. Otolith nerve stimulation also evoked monosynaptic EPSPs in 17 of the 29 neurons. In the remaining 12 VS neurons, polysynaptic compound PSPs were evoked in response to stimulation of the PC and otolith nerves. Saccular neurons alone were found more frequently that of utricular neurons alone among VS neurons (Fig. 1). PC-alone VS neurons had a similar ratio (38/104, 37%) to that of convergent neurons. Axons of about two-thirds of the VS neurons (including both convergent and non-convergent) descended in to the LVST.

V neurons

These neurons may send axons to the contralateral, as well as ipsilateral vestibular nuclei, the reticular formation and the cerebellum. However, these V neurons were not activated after stimulation of the oculomotor nuclei and the spinal cord at an intensity of ~ 2 mA. Twenty-nine neurons had convergent inputs from the PC and otolith nerves. Five of the 29 V neurons were activated monosynaptically following stimulation of the PC and the otolith nerves. The majority of the remaining V neurons received monosynaptic inputs from the PC nerve and polysynaptic

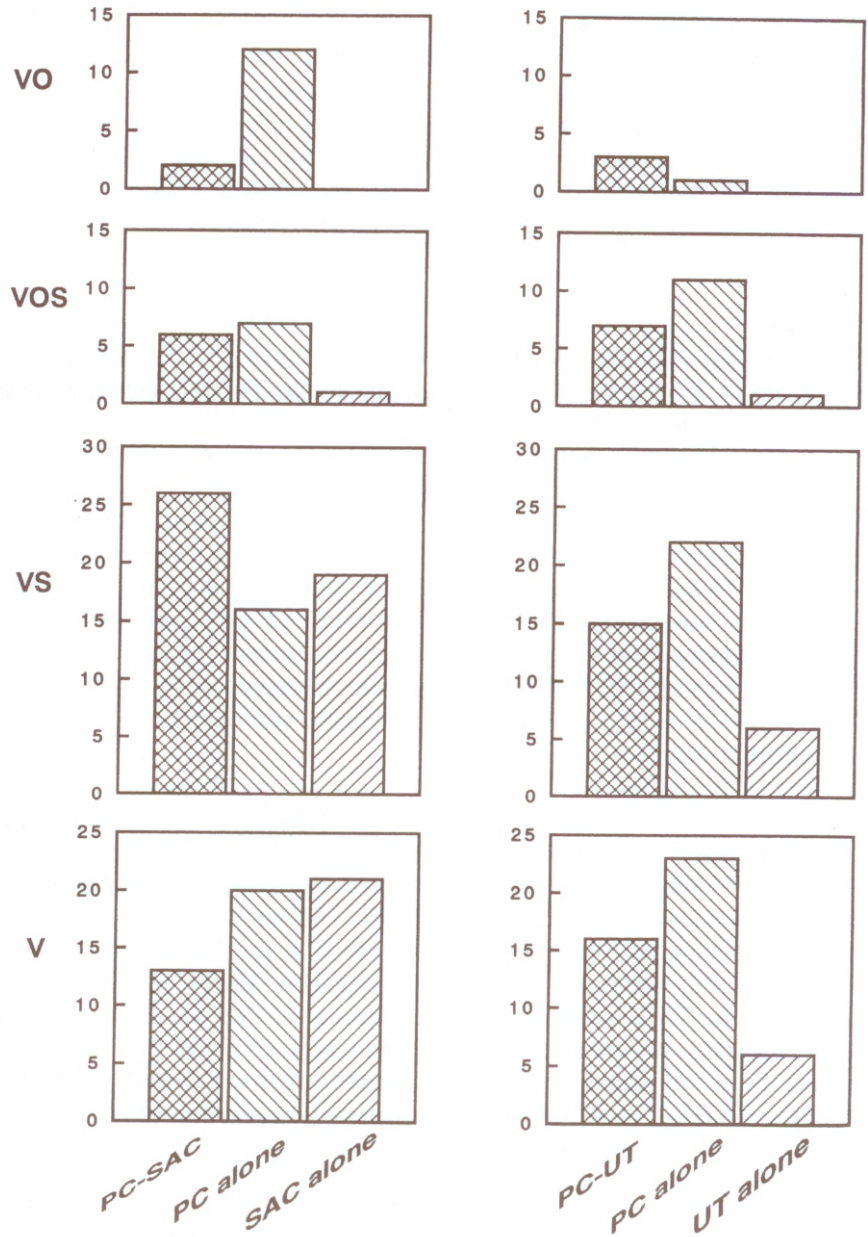

Fig. 1. - *Histograms of vestibular neurons with or without input converge from the posterior canal and saccular nerves, and those from the posterior canal and the utricular nerves.*

Vestibular neurons are classified according to the axonal target. Ordinates indicate number of neurons.

Abbreviations: PC, posterior canal; SAC, saccular; UT, utricular; V, vestibular neurons without ascending or descending axon collaterals to the oculomotor nuclei or the spinal cord; VO, vestibulo-ocular neurons without descending axon collateral to the spinal cord; VOS, vestibular neurons with ascending and descending axon collaterals to the oculomotor nuclei and spinal cord; VS, vestibulospinal neurons without ascending axon collaterals to the oculomotor nuclei.

compound inputs from the otolith nerves, or vice versa. The ratio of saccular neurons alone was higher than that of utricular neurons alone (Fig. 1). V neurons that received only PC input were abundant (Fig. 1).

DISCUSSION

Convergence of primary afferents from the PC and otolith macula on single vestibular neurons were studied, classifying vestlbular neurons as VO, VOS, VS and V neurons according to their antidromical activation from the oculomotor nuclei and spinal cord. This study consisted of two series of experiments; convergence of PC and utricular inputs were examined in one series, and PC and saccular inputs in the other. In the former series, since convergence from the saccule was not examined, the recorded vestibular neurons may have received saccular inputs. Similarly, the vestibular neurons recorded in the later series may have had utricular inputs. Therefore, the neurons identified as PC alone neurons may have had otolithic input that was not tested in individual experiments, and thus the number of PC alone neurons could be overestimated. Even taking this in account, however, otolith-activated neurons sending axons to the oculomotor nuclei (VO and VOS) were few. In particular, secondary vestibular neurons monosynaptically activated by otoloth stimulation rarely sent axons to the oculomotor nuclei (i.e. VO or VOS neurons), but mostly sent axons exclusively to the spinal cord (i.e. VS neurons).

Vestibulo-ocular reflex pathway from the posterior-canal and the otolith organs

Recently, we have found monosynaptic connections from the utricular nerve to motoneurons and interneurons in the abducens nucleus (11, 40). We also studied connections from the utricular nerve to motoneurons of all extraocular muscles (27, 40, 45). These studies elucidated that the disynaptic pathway from the utricular nerve to extraocular motoneurons, except for abducens motoneurones and interneurons, is poorly organized. Stimulation of the utricular nerve evoked depolarizing and hyperpolarizing potentials with longer latency in contralateral and ipsilateral medial rectus motoneurons, and complex potentials with longer latencies in ipsilateral inferior oblique and contralateral trochlear motoneurons (27, 45). These longer latency reflex pathways were considered to be trisynaptic or more synapse-mediated on the bases of our latency analyses (27, 37, 38, 40, 45). Recently, we also studied connections between the saccular afferents and individual motoneurons of all the extraocular muscles (13). The results showed that the sacculo-ocular reflex pathways have more poorly organized connections than the utriculo-ocular connectivity.

Axonal projections of utricular nerve-activated vestibular neurons to the oculomotor nuclei and the spinal cord were also studied. Almost no second order vestibular neurons, monosynaptically activated by utricular nerve stimulation, had ascending branches to the oculomotor nuclei (28). Few VO and VOS neurons which were activated monosynaptically from the utricular nerve or the saccular nerve were found in the present study. All the VO neurons which received either

saccular or utricular input also received PC input (Fig. 1). Only two VOS neurons, which received polysynaptic input from the utricular or the saccule but, no input from the PC, sent axons to the oculomotor nuclei (Fig. 1). However, there is a possibility that they may have received input from the anterior canal, but this was not tested. Thus, the otolith-ocular reflex arcs, except those concerned with horizontal eye movement, seem not to have their own independent pathways, but to share a part of the canal-ocular reflex pathways. It is interpreted that the common pathways are available since the combination of vertical canals activated by rotational angular acceleration, and parts of the otolithic organs activated by gravitic acceleration, are always used during head inclination, unless the head is upside-down. The present results, together with our previous data (13, 27, 40, 45), strongly suggest that the three neuron arcs from the utricular and saccular nerve to the extraocular motoneurons, except abducens motoneurons, are very poorly organized.

Vestibulocollic reflex pathway from the posterior canal and otolith organs

Using of selective stimulation of the semicircular canal nerves and saccular and utricular nerves, connections from canal nerves (14, 15, 32, 35, 36, 41-43) and utricular nerves (2, 10), and saccular nerves (48) to neck extensor and flexor motoneurons were studied. Saccular and utricular nerve inputs in motoneurons innervating the sternocleidomastoid muscles (SCM) were also studied (20). These data are summarized in Table 1. Ipsilateral SCM motoneurons generated IPSPs with the same range of (i.e., disynaptic) latency after activation of the PC as the saccular and utricular nerves through the same pathway, i.e., MVST. Similarly, contralateral SCM motoneurons frequently generated disynaptic EPSPs after PC and utricular nerve stimulation via the same pathway (MVST). Contralateral extensor motoneurons also generated identical potentials (disynaptic IPSPs) after both types of stimulation, although the pathway from the utricular nerve to the spinal motoneurons is unknown. The present study found lots of second order VS neurons which were activated monosynaptically from both the PC and saccular nerve or from both the PC and utricular nerve. It is very likely that they mediate

Table 1. - *Postsynaptic potentials (PSPs) evoked by stimulation of the posterior-canal, saccular and utricular nerves in ipsilateral and contralateral neck extensor, flexor and sternocleidmastoid motoneurons.* Preceding numbers indicate the number of inter synapses. The lower rows indicate pathways.

	Ipsilateral			Contralateral		
	Extensor	Flexor	SCM	Extensor	Flexor	SCM
Sacculs	2-EPSP LVST	2-IPSP MVST	2-IPSP MVST	2-EPSP MVST	3-IPSP MVST	No input
Utricul.	2-EPSP Not tested	2-EPSP LVST	2-IPSP MVST	2-IPSP Not tested	3-IPSP LVST	2-EPSP MVST

Extensor rnuscles, rnainly biventer cervicis and complex; Flexor muscles, longus capitis; SCM muscle, sternocleidmastoid; 2- and 3-, di- and tri-synaptic; EPSP, excitatory postsynaptic potential; IPSP, inhibitory postsynaptic potential; M and LVST, medial and lateral vestibulospinal tract.

the above pathways and partly contribute to the generation of disynaptic potentials. Inhibitory VS neurons with monosynaptic convergence from the PC and utricular nerves seem to innervate ipsilateral SCM or contralateral extensor motoneurons via the MVST. Those from the PC and the saccular nerves very likely innervate ipsilateral SCM motoneurons via the MVST. They are thought to be located in the ventral part of the lateral vestibular nucleus and the rostral part of the descending nucleus, since it is known that PC-activated inhibitory vestibulospinal neurons are also located there (14, 15) and that utricular and saccular afferents principally project in the same area (5, 11, 12, 19, 21, 33). On the other hand, excitatory VS neurons with monosynaptic convergence from the PC and the utricular nerves seem to innervate contralateral SCM via the MVST. It is hypothesized that these convergent VS neurons function conveniently to stabilize the head position when the head is inclined near the normal (i.e., upright) position, since convergent inputs from the semicircular canal and the otolith organ make them sensitive to head inclination. Convergent VS neurons that receive monosynaptic or polysynaptic PC input and polysynaptic otolithic input may also contribute to the same function by modulating the direct pathways. VS neurons receiving either PC or otolithic input seem to contribute to specific reflexes. Neck motoneurons, in particular, in which different types of postsynaptic potential are evoked after PC and otolithic nerve stimulation (see Table), must be innervated by the non-convergent neurons. However, note that VS neurons which were classified as non-convergent neurons receiving otolithic input, but no PC input, in the present study, may have received anterior canal inputs and mediated both inputs to the neck motoneurons.

The ratio of convergent neurons with PC input among all utricular nerve-activated VS neurons was higher than the ratio of convergent neurons among saccular nerve-activated VS neurons (Fig. 1). This seems to reflect a difference in number of neck motoneuron groups that receive inputs from the PC and utricular nerves being greater more than those receiving identical inputs from the PC and saccular nerves (Table 1). The consistency of these two comparisons suggests that motoneurons receiving identical inputs from the canal and otolith nerves are frequently innervated by convergent neurons. In contrast with PC input, more groups of neck motoneurons received the same inputs from the anterior semicircular canal and saccular nerves, compared with those receiving the same inputs from the anterior canal and utricular nerves. Thus, it is possible to estimate that the ratio of convergence with anterior canal input on single VS neurons is higher among saccular nerve-activated neurons than utricular nerve-activated neurons.

Recently, we studied the pathways of otolith-activated VS neurons using extracellular recording during stimulation of the spinal cord (29). The majority of utricular nerve-activated VS neurons gave off axons to the spinal cord through the LVST. This was consistent with the present results. On the other hand, more than half of saccular nerve-activated VS neurons sent axons through the MVST, while two-thirds gave off axons through the LVST in the present study, according to intracellular recording from vestibular neurons. Since intracellular recording from small cells is relatively more difficult compared with extracellular recording, this discrepancy may result from the recording techniques.

SUMMARY

Convergence of both afferents from the PC and saccular macula, and those from the PC and utricular macula on single vestibular neurons was noted by use of intercellular recording from vestibular neurons. Vestibular neurons were classified VO neurons (vestibulo-ocular proper neurons), VOS (Vestibulo-oculo-spinal neurons sending axon collaterals both to the extraocular motoneuron pools and to the spinal cord), VS neurons (vestibulospinal proper neurons) and V neurons (vestibular neurons without axons to the oculomotor nuclei or the spinal cord) on the basis of whether or not they responded antidromically to stimulation of the oculomotor nuclei and the spinal cord. Of the total 143 vestibular neurons recorded in the series of experiments on convergence of the PC and saccular afferents, 47 neurons (33%) were received inputs from both the PC and saccular nerves. Twenty-six of the 47 convergent neurons were identified as having the nature of VS neurons. Half (13/26) of those were activated monosynaptically from both the PC and saccular nerves. Only one saccular-activated neuron without PC inputs sent an axon to the oculomotor nuclei.

In the other series of experiments on the convergece of the PC and utricular afferents, 41 (37%) of 111 vestibular neurons were proved to converge on inputs from both nerves. The majority (35/41) of the neurons received monosynaptic inputs from the PC nerve and polysynaptic EPSP-IPSP sequences from the utricular nerve, or vice versa. The ratio of PC-otolith convergent neurons among utricular-activated neurons (41/54, 76%) was higher than that among saccular activated neurons (47/88, 53%). The percentage of utricular alone neurons without PC inputs (13/111, 12%) was less than that of the saccular alone without PC inputs (41/145, 28%). In conclusion, the convergence of canal and otolith inputs likely contribute mainly to vestibulospinal reflexes including the vestibulocollic reflex, by sending inputs to the neck and other muscles during head inclination which creates the combined stimuli of angular and linear acceleration.

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