Neurologia medico-chirurgica, Vol. 18, Part I, 1978, 5–16

The Neck, the Labyrinth, the Cerebellum and Posture

Minoru MAEDA and Shozo ISHII

Department of Neurosurgery, Juntendo University
Tokyo, Japan

Summary

Neuronal organizations between the labyrinth, the neck, and vestibulo-cerebellum were investigated in the cat.

Disynaptic excitatory postsynaptic potentials (EPSPs) and inhibitory postsynaptic potentials (IPSPs) were recorded in dorsal neck extensor motoneurons in response to stimulation of individual ampullary nerves. Stimulation of the saccular nerve usually evoked IPSPs in contralateral and EPSPs in ipsilateral neck motoneurons. Many potentials probably were trisynaptic. The predominant pattern produced by utricular nerve stimulation consisted of ipsilateral inhibition and contralateral excitation and many potentials were disynaptic.

Afferent volleys from the neck joint ascend ipsilaterally in the spinal cord, cross to the contralateral side in the brain stem, and project to the vestibular nuclei interacting with the vestibulo-ocular reflex activity. EPSPs or IPSPs were evoked in abducens motoneurons by stimulation of contralateral or ipsilateral neck joint, respectively.

Stimulation of neck afferents causes activity in the flocculus by a climbing fiber (CF) and also by a mossy fiber (MF) route. In the rostral half of the flocculus, field potentials were recorded in response to stimulation of the neck, vestibular and optic nerves. Neck afferents project also to the nodulus.

With regard to MF pathways, neck activity arises, at least in part, in joint receptors and the relay is located in Brodal and Pompeiano's group X.

Key words: Posture, neck proprioceptors, vestibular nuclei, oculomotor system, vestibulocerebellum, eye movement.

Introduction

Since the poineer work of Magnus,[23] there has been several investigations on the role of neck proprioceptors in postural adjustment and their close relation to vestibular function (Cohen,[6] Fredrickson et al.,[10] and Biemond and De Jong[2]). Neck proprioceptors also play an important role in the control of eye position (Magnus,[23] Suzuki and Takemori[31]). Twisting of the neck and body produces eye deviation in the rabbit as well as in the man. It is pointed out that patients suffering cervical injuries (whiplash) have several disturbances in maintaining body equilibrium or eye position with or without vegetative concomitants (Ishii[17]). Recently, attention has been paid to elucidate a pathogenesis of the static and the dynamic equilibrum disturbances in patients with cervical injuries on the basis of clinical neurophysiology (Hinoki,[15] and Imai et al. [16]). The purpose of this experiment was three-fold: 1) Determination of the pattern of effects evoked from the labyrinth that might serve as the basic circuit for the reflexes of equilibrium, vestibulo-neck reflex; 2) Investigation of the pattern of cervical inputs to the oculomotor system and vestibular nuclei; and 3) Elucidation of mode of neck afferent inputs to the cerebellum that might adjust the body equilibrium and control eye movement.

Methods

Experiments were performed on adult cats. Animals were initially anesthetized by intravenous injection of 0.5% sodium thioamytal (surital, Parke, Davis) in normal saline. Surgical procedures were usually completed under halothane, then the cats were paralyzed by intravenous injections of galamine triethiodide (Flaxedil) under artificial respiration and bilateral pneumothorax was induced routinely to improve instability. Blood pressure was monitored from one femoral artery and, when necessary, maintained between 100 and 120 mmHg by intravenous infusion of metaraminol bitartrate (Aramine) in normal saline. The rectal temperature was kept at 36–38°C by radiant heat.

1) *Semicircular, saccular and utricular inputs to dorsal neck motoneurons*
Bipolar stimulating electrodes made of insulated 40 μ stanless steel wire were inplanted near the ampullary nerves as described by Suzuki et al.[30]. In order to stimulate maculae, sacculus and utriculus, selective transection of the vestibular nerve branches with preservation of saccular or utricular nerve fibers was performed. For preservation of the saccular nerve (Fig. 2A1), the entire superior vestibular division and posterior ampullary nerve were transected at the level of scarpa's ganglion.[40] For selective preservation of the utricular nerve branch, the entire posterior inferior vestibular division and the rostral one-half of the superior vestibular division were transected as shown in Fig. 2B1. Survival periods of 27–179 days were required for postoperative recovery in these animals.

The C_2 and C_3 segments were exposed by dorsal laminectomy to permit intracellular recording from motoneurons. Conventional circuits were used to record and pass current through the microelectrode. Motoneurons were identified by antidromic stimulation of muscle nerve. Neck nerves dissected were those to splenius (SP) and the dorsal rami (DR).

2) *Cervical input to abducens motoneurons and second order vestibular nuclei neurons*
Stimulating electrodes (a fine Ag-AgCl wire) were placed on the vestibular nerve [29] and in the region of the upper neck joints.[14,18] In other experiments, the cervical dorsal roots (C_2–C_4) were stimulated after a laminectomy. Intracellular recording from abducens motoneurons or extracellular recording of the spikes of the vestibular neurons were performed with glass micropipettes filled either with 3M KCl or Ringer solution, respectively.

3) *Cervical input to the vestibulocerebellum*
After surgical procedure under anesthesia with halothane, the anesthesia was replaced during recording by a N_2O–O_2 mixture. The flocculus or the nodulus was approached dorsoventrally, usually through the paraflocculus or the posterior vermis. The ipsilateral vestibular nerve, bilateral optic nerves (sometimes contralateral optic disc) and neck afferents (upper dorsal rami and C_2–C_4 dorsal root ganglia) were stimulated. Field potentials were recorded both in the flocculus and in the nodulus with glass microelectrodes filled with NaCl saturated with fast green (FCF)[32] and were routinely computer-averaged.

4) *Mossy fiber cervical projections to the flocculus*
The vestibular nerve was stimulated ipsilaterally with implanted bipolar electrode. The dorsal rami (DR) of the ipsilateral C_2 and C_3 nerves, as well as the C_2 dorsal root ganglion, were exposed and placed on bipolar platinum electrode (Fig. 9A). The stimulating electrode array consisting of two tungsten wires, about 1 mm apart, was placed rostrally in the flocculus in, or at the base of, a granular layer (Fig. 9B). Field potentials that could be recorded with the array were usually monitored at different stages of the experiment to check for displacement of the stimulating electrodes. At the end of the experiment lesions were made by passing 20 μA of cathodal current through each electrode for 20 sec.

The caudal part of the vestibular nuclear complex was approached dorsocaudally, after removal of the most caudal part of the cerebellum. Extracellular recording, with electrodes filled with 2*M* NaCl saturated with fast green FCF,[32] was performed.

Results

(I) Semicircular, saccular and utricular inputs to dorsal neck motoneurons

Stimulation of ipsilateral and contralateral ampullary nerves evoked EPSPs and IPSPs in all neck motoneurons innervating dorsal neck muscles (SP & DR)(Fig 1). The latency of the earliest component of EPSPs and IPSPs ranged from 1.7 to 2.8 msec and was usually less than 2.5

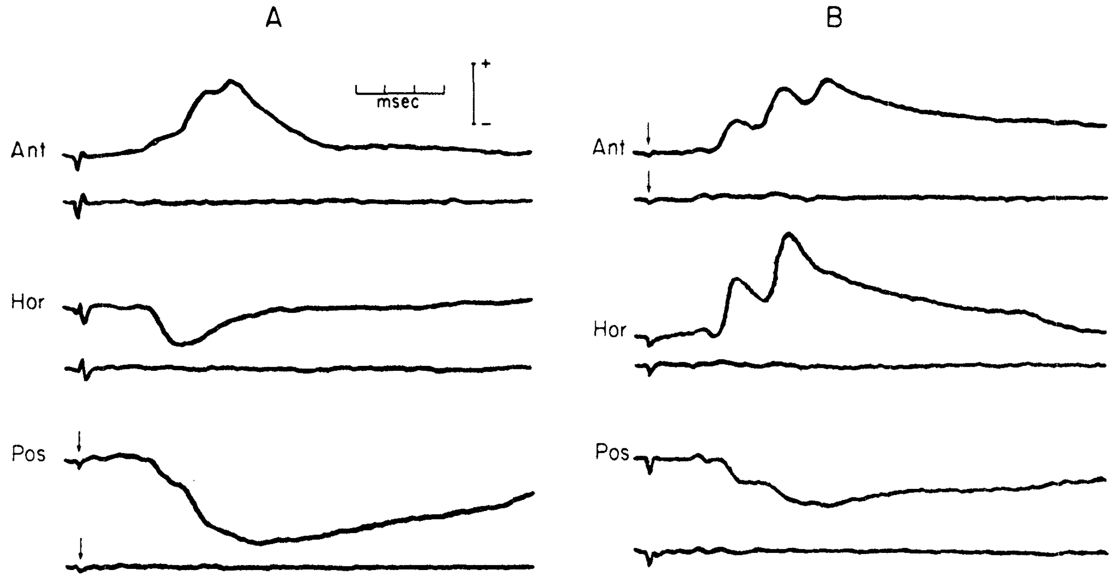

Fig. 1 Pattern of synaptic potentials evoked in dorsal neck motoneurons by stimulation of ipsilateral and contralateral ampullary nerve. In each frame the upper trace shows the computer averaged intracellular response, the lower trace the extracellular field potential.
A) Potentials evoked in a DR motoneuron by ipsilateral stimulation. Ant; anterior canal, Hor; horizontal canal, Pos; posterier canal
B) Potentials produced in a DR motoneuron by contralateral stimulation. Arrows indicate time of stimulus. Voltage calibration 500 μV except for Ant in B, where it is 1 mV.[36)]

msec. These latencies are similar to those obtained with whole nerve stimulation and shown to be disynaptic.[33)] The pattern of connections between different ampullae and motoneurons was quite stereotyped as shown in Fig. 1. Dorsal ramus motoneurons were excited by stimulation of the two anterior canals, and inhibited from two posterior canals. These motoneurons may also be inhibited from the ipsilateral, excited from the contralateral horizontal canal. Splenius motoneurons were influenced most consistently from the horizontal canal. The lesion experiments showed that the pathways connecting the ampullae to neck motoneurons could be summarized as shown in Fig. 3: all inhibitory fibers are in the medial vestibular nucleus solitary tract (MVST), as are contralateral excitatory fibers; ipsilateral excitatory fibers are in the lateral vestibulo-spinal tract (LVST).

Stimulation of the saccular nerve usually evoked IPSPs in contralateral, EPSPs in ipsilateral dorsal neck motoneurons such as those illustrated in Fig. 2. Some of the potentials were disynaptic, many were later and probably trisynaptic. Although, the effects of utricular nerve stimulation were complex, the predominant pattern consisted of ipsilateral inhibition and contralateral excitation. This pattern is opposite to the effects of saccular nerve stimulation. Many potentials induced from the utricular nerve were disynaptic.

(II) Cervical input to abducens motoneurons and second order vestibular nuclei neurons

1) *PSPs evoked in abducens motoneurons by neck stimulation*

Fig. 4A shows the antidromic response to stimulation of the right abducens nerve.[1)] Contralateral dorsal root (C_2 or C_3) stimulation produced a hyperpolarizing potential in the abducens motoneurons. As stimulus strength or number of stimulus pulses was raised, the potentials increased in amplitude (Fig. 4B D). The hyperpolarization was increased by depolarization and decreased or reversed by passing hyperpolarizing currents or Cl^- ions injection through the recording microelectrode (Fig. 4C). Thus the hyperpolarization should represent an IPSP (Eccles[8)]). Similar IPSPs were produced by stimulation of the contralateral neck joint.

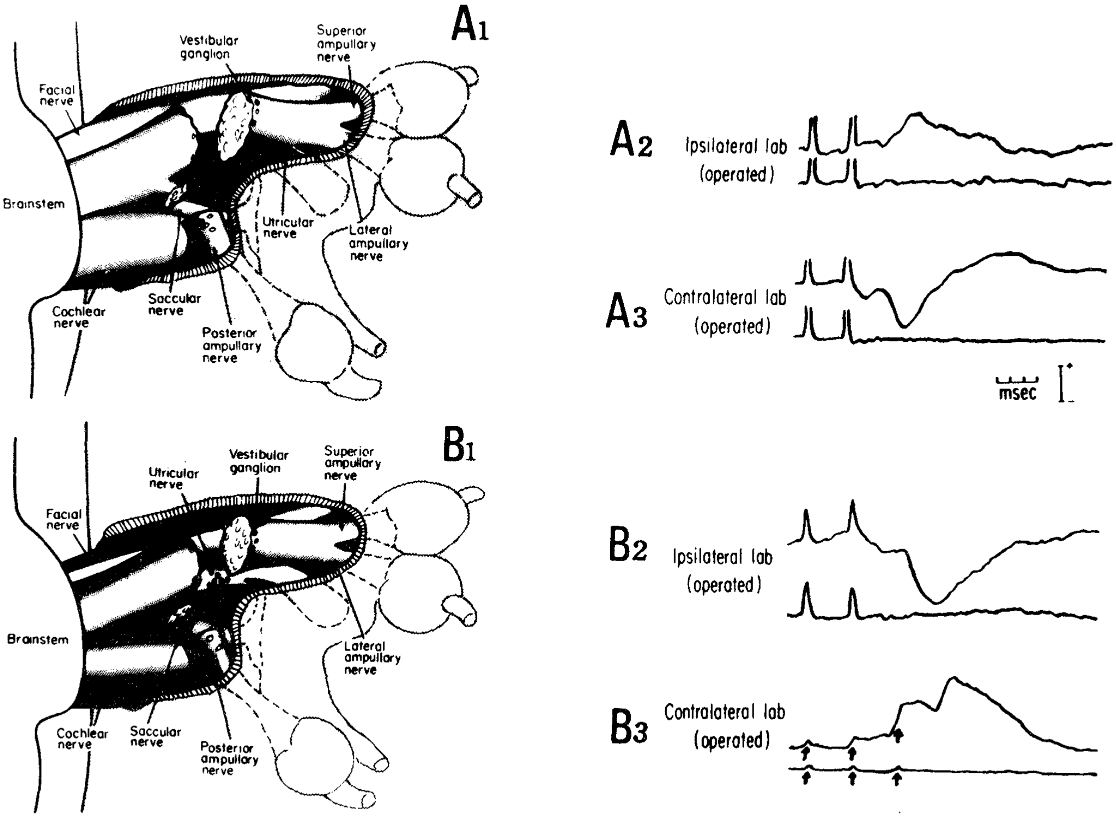

Fig. 2 Drawings of the transected vestibular nerve branches (dorsal view of right side) and synaptic potentials produced in DR motoneurons by stimulation of the vestibular nerve. A_1 : selective preservation of the saccular nerve. A_2 and A_3 : synaptic potentials evoked by stimulation of ipsilateral (A_2) and contralateral (A_3) saccular nerve. B_1 : selective preservation of the utricular nerve. B_2 and B_3 : synaptic potentials evoked by stimulation of ipsilateral (B_2) and contralateral (B_3) utricular nerve. Each trace shows computer-averaged synaptic potentials (25–50 sweeps). Lower traces, extracellular field potentials. Voltage calibration, 500 μV.[40)]

The latencies of the IPSPs ranged from 2.8 to 6.0 msec from the dorsal root and 3.0 to 7.5 msec from the neck joint.

Ipsilateral dorsal root stimulation produced a depolarization in abducens motoneurons. The depolarization increased in amplitude and longer in duration with increased stimulus strength or number of stimulus pulses (Fig. 4D). The depolarizing potential did not change after Cl^- ion injection into the motoneuron (Fig. 4E) and was an EPSP. Similar EPSPs were induced after ipsilateral neck joint stimulation.

The latencies of the EPSPs ranged from 2.8 to 5.3 from the dorsal root and 3.2 to 7.3 msec from the neck joint.

The latencies of the EPSPs and IPSPs distribute within approximately the same range

2) *Interaction of neck and vestibular effects in abducens motoneurons*

Stimulation of the ipsilateral vestibular nerve produces a disynaptic IPSP in the abducens motoneurons and the interneurons are located mainly in the medial vestibular nucleu.[1)] The interaction of IPSPs evoked by stimulation of the ipsilateral vestibular and cervical nerve was studied. Fig. 5A exemplifies the mode of interaction and illustrates a control disynaptic IPSP (reversed in polarity after Cl^- injection) in an abducens motoneuron produced by ipsilateral vestibular nerve stimulation. As conditioned by contralateral neck stimulation that was so adjusted as to produce only a small IPSP (Fig. 5Ab), the same vestibular volley evoked a larger disynaptic IPSP (Fig. 5Ac) than the algebraical summation (dotted line in AC). Similar results were obtained when the interaction of contralateral vestibular and ipsilateral neck nerve evoked EPSPs were studied. Impulse activity was recorded within the abducens nucleus from axons that are presumed to have their origin in the vestibular nuclei. Of 28 units activated from

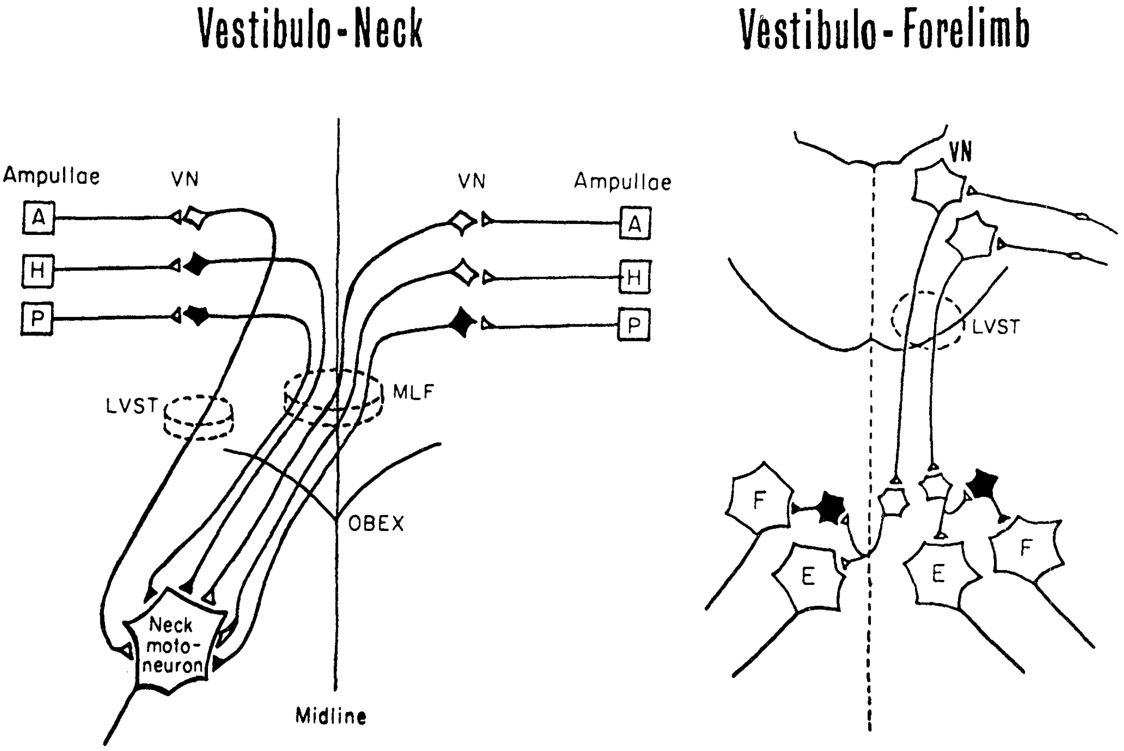

Fig. 3 Schematic of simplified pathways of the vestibulo-neck and the vestibulo-forelimb reflex arch.
Abbreviations: A.H.P., anterior, horizontal, and posterior ampulae. VN, vestibular nuclei. MLF, medial longitudinal fasciculus. LVSF, lateral vestibulospinal tract. E, extensor forelimb motoneuron. F, flexor forelimb motoneuron. Inhibitory neurons are filled in black and excitatory neurons are open.[20,36]

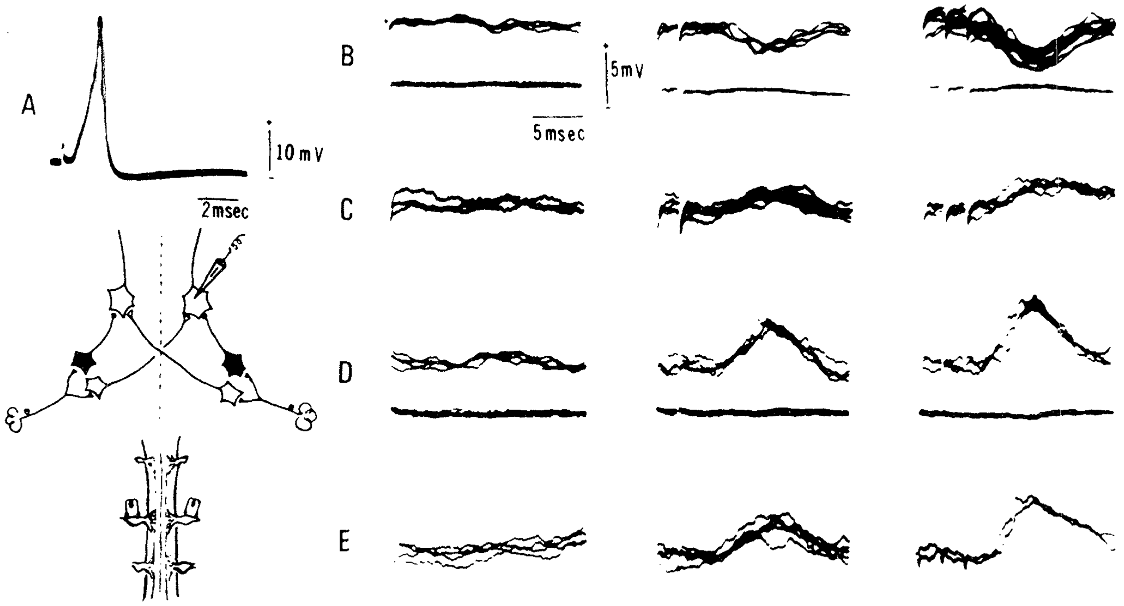

Fig. 4 Synaptic potentials evoked in abducens motoneurons by stimulation of ipsilateral and contralateral dorsal root ganglia (C_2).
A) Antidromic response to stimulation of right abducens nerve. Lowers, schematic drawing of experimental arrangement.
B) IPSPs produced by stimulation of the contralateral C_2 ganglion as the number of stimulus pulses increased from single to triple.
C) Same as in B but reversed IPSPs due to Cl^- injection.
D) EPSPs induced by ipsilateral C_2 ganglion stimulation (with single to triple shocks).
E) Same as in D but after Cl^- injection. Voltage calibration and time scale for B applies to others.[14,19]

ipsilateral vestibular nerves, 25 units were excited by contralateral dorsal root or neck joint stimulation. These results indicate that the facilitatory interaction occurred at the level of the excitatory and inhibitory interneurons in the vestibular nuclei.

3) *Activity of vestibular Type-1 neurons in response to neck volleys*

Neurons in the vestibular nuclei were identified by horizontal angular acceleration and deceleration. Type-1 neurons were defined by their frequency responses to horizontal rotation in parallel with receptor activities in the ipsilateral horizontal canal.[12)] The Type-1 neuron was facilitated in response to contralateral neck joint stimulation (Fig. 5B). On the other hand, long train shocks to the ipsilateral neck joint produced an inhibition of spontaneous discharges of Type-1 neurons. These results on vestibular neuron responses provide further support to the view that the facilitatory interaction between the vestibulo-abducens and cervico-abducens reflexes occurs in the vestibular nuclei.

(III) Cervical input to the flocculus and the nodulus

We recorded field potentials induced from vestibular and optic nerve stimulation throughout the rostral half of the flocculus. The recording area was identified by fast green dye marks in frozen sections. It has been described that field potentials of vestibular origin are produced by the mossy fiber (MF) route in the cat[27)] and the pigeon.[35)] On the other hand, potentials of visual origin are evoked by the climbing fiber (CF) route in the flocculus of the rabbit[22)] and the cat.[37,38)] Fig. 6Bc shows field potentials evoked by stimulation of the C_3 ganglion. Field potentials produced by stimulation of the vestibular nerve (Fig. 6Ba) or optic nerve (Fig. 6Bb) are illustrated as compared with neck evoked potentials. In this and almost every other instance the field potentials produced by stimulation of neck afferents had depth profile similar to those of optic nerve-evoked potentials (compare Fig. 6Bb with Bc): A positivity in the granular layer and a

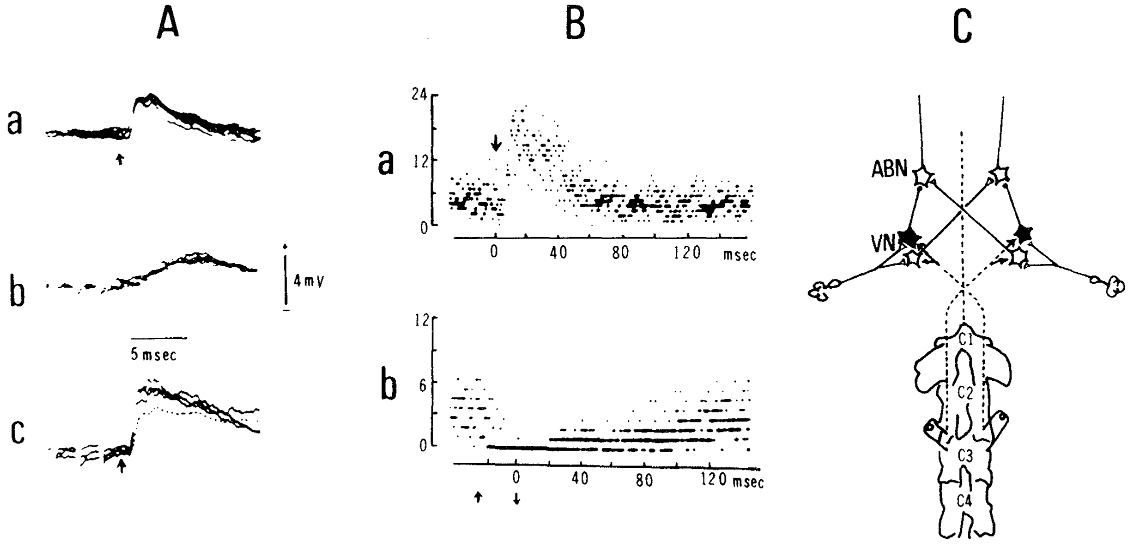

Fig. 5

A) Facilitation of the vestibular induced disynaptic IPSPs by cervical stimulation.
Aa, disynaptic IPSPs (reversed after Cl^- injection) evoked in an abducens motoneuron by stimulation of the ipsilateral vestibular nerve.
Ab, response to contralateral dorsal root stimulation.
Ac, the same test stimulation as in Aa was conditioned by cervical stimulation, dotted line indicates an algebraical summation of Aa and Ab.
B) Activity of vestibular Type-1 neurons in response to cervical stimulation.
Ba, Spike distribution for a Type-1 neuron constructed from 300 sweeps following stimulation of the contralateral neck joints.
Bb, Spike distribution obtained by ten shocks to ipsilateral neck joint.
C) Schematic drawing of simplified connections between upper cervical afferents and abducens motoneurons and second order vestibular neurons.[14,19)]

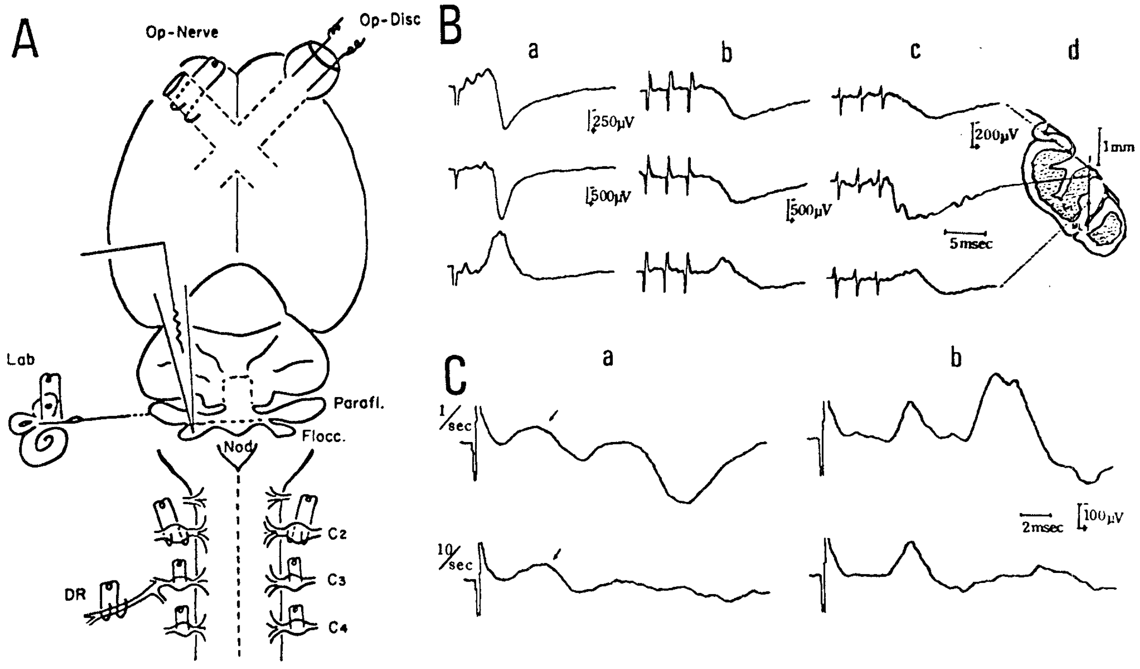

Fig. 6. Depth profile of potentials in the flocculus.
A) Experimental arrangement.
B) A, b and c; field potentials evoked in the granular and the molecular layer of the flocculus by stimulation of ipsilateral labyrinth (Ba), optic nerve (Bb) and Cb ganglion (Bc), respectively. Potentials in each row were recorded at the location indicated by the filled circle in Bd.
C) MF and CF responses produced in the flocculus following stimulation of the ipsilateral C_3 ganglion. a,b: recorded in the granular (a) and in the molecular (b) layer, respectively.[37)]

negativity in the molecular layer. Such a profile is the same as previously reported for a CF input.[22)] In contrast to a CF profile, vestibular nerve-evoked field potentials as shown as the typical MF profile (Fig. 6Ba): an N_2P_2 in the granular layer and N_3 in the molecular layer. When the frequency of stimulation was raised from 1/sec, both neck- and optic nerve-evoked field potentials were usually strongly depressed at stimulus frequencies of 10–20/sec, whereas vestibular-evoked potentials were not affected. Susceptivity to frequencies of 10–20/sec is further evidence that impulses in neck afferents reach the flocculus by the CF route.[9)]

In some experiments we observed the presence of a MF input from neck afferents to flocculus. Fig. 6C illustrates the different frequency sensitivity of neck-evoked MF and CF responses; the early potentials in the granular and molecular layers are essentially unaffected when the frequency of stimulation is changed from 1/sec to 10/sec, whereas the later potentials (CF) are abolished. The onset of the N_2 was usually at 2.0–3.0 msec, and the latency of the N_3 was 4.0–6.0 msec.

A cut of dorsal column at the C_2 level was made in three experiments, with results such as those illustrated in Fig. 7. After transection the field potential evoked by stimulating neck afferents on that side was abolished, suggesting that the DF-SOCP is an important link between neck and ipsilateral flocculus. Contralateral potentials could not be abolished by any limited lesion.

Stimulation of the C_2 dorsal ganglion-evoked field potentials in the nodulus. Figure 8C and E show neck-evoked potentials in the molecular and upper granular layer of the nodulus, respectively. These field potentials had depth profiles similar to those evoked by vestibular stimulation (Fig. 8B and D) and may, therefore, be ascribed to the mossy fiber pathways. In contrast to the flocculus, which received MF-and CF-inputs from upper cervical regions, no CF-evoked field potentials were seen in the nodulus after C_2 ganglion stimulation.

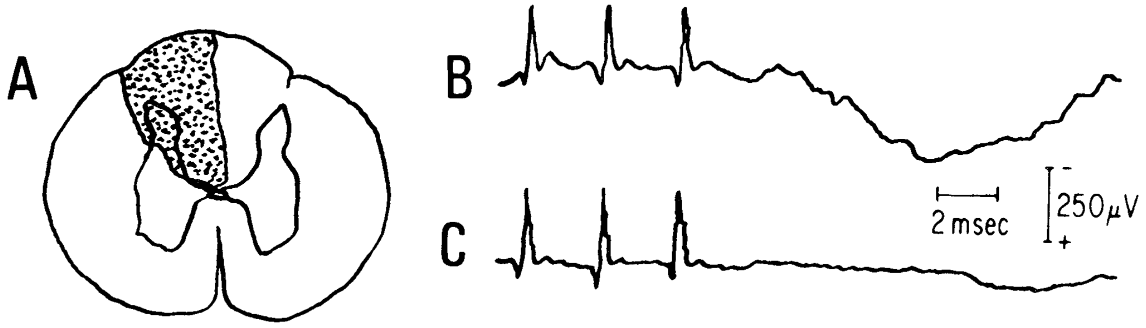

Fig. 7 Effect of dorsal colum cut on the response to ipsilateral C_3 ganglion stimulation.
A) Lesion is shown by the dotted area.
B) Field potential recorded in the granular layer by stimulation of the ipsilateral C_3 ganglion before the cut.
C) Same as in B) but after the cut.[37)]

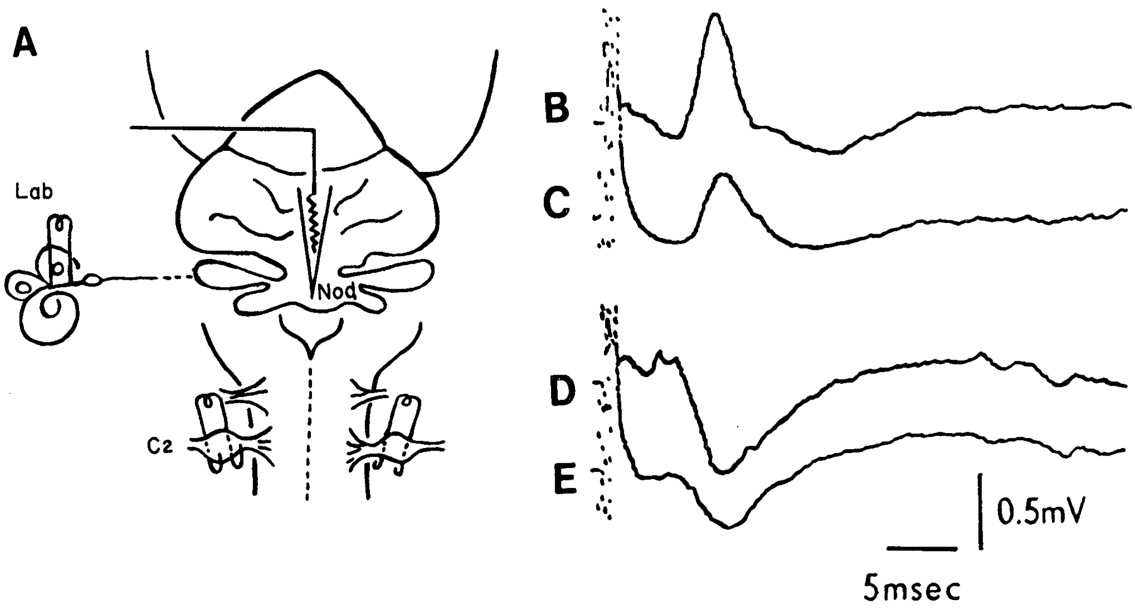

Fig. 8 Depth profile of response to vestibular and cervical stimulation.
A) Experimental arrangement
B), C) Field potential evoked in the molecular layer of the nodulus following stimulation of the vestibular B) and the C_2 ganglion (C), respectively.
D), E) Same as in B) and C) but recorded in the upper granular layer of the nodulus.[28)]

(IV) Mossy fiber cervical projections to the flocculus

Fig. 9A is a diagram of the experimental arrangement. Antidromic responses were identified by fixed latency, response to frequencies of stimulation as high as 500/s and collision block of the antidromic impulse by orthodromically evoked spikes.

Stimulation of the ipsilateral C_2 ganglion caused firing of many single units which often responded to one stimulus with two to three impulses. Twenty-seven neurons were studied that responded to stimulation of the C_2 ganglion. These neurons were fired antidromically at latencies of 0.4–1.0 msec after floccular stimulation. The response of a typical cell is shown in Fig. 9C. The same unit responds antidromically to floccular stimulation (Fig. 9C1) and orthodromically to C_2 ganglion stimulation (Fig. 9C2). When the second orthodromic spike precedes the antidromic spike by an interval less than twice antidromic conduction time plus refractory period (Fig. 9C4) the antidromic response is blocked by collision. The earliest orthodromic la-

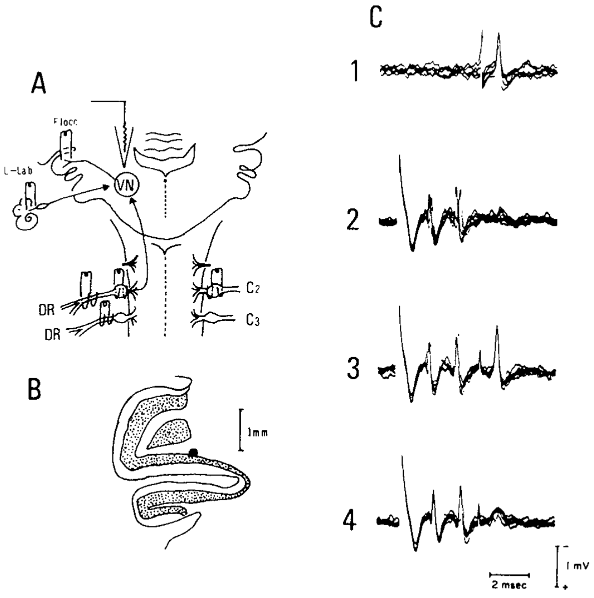

Fig. 9 Response of brain stem neuron to stimulation of the C_2 ganglion

A) Experimental arrangement.

B) Location of one of a pair of electrodes placed in the flocculus, identified by an electrolytic lesion. The lesion is represented by a black dot.

C) 1: Antidromic response to flocculus stimulation
   2: Stimulation of the C_2 ganglion
   3: Stimulus to the ganglion precedes flocculus stimulation
   4: The antidromic spike is blocked by collision at a close stimulus interval.[39)]

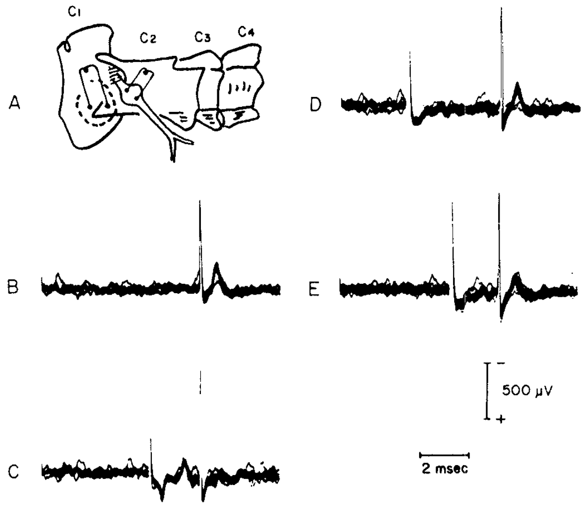

Fig. 10 A cell activated by stimulation of neck joint afferent.

A) Bipolar electrodes were placed on the area of the atlanto-axial joint and on the C_2 ganglion.

B) Antidromic spike evoked in the brain stem by stimulation of the flocculus.

C) The same neuron is fired by stimulation of the joint area, as shown by collision block of the antidromic response.

D) and E) After an incision around the stimulus area as shown in A) the neuron is no longer fired by stimulation and no collision block at a closer interval E).[39)]

tency ranged from 1.3 to 2.0 ms, 0.5–1.1 ms later than the positive peak of the afferent volley, thus indicating that most if not all the neurons responded monosynaptically to C_2 ganglion stimulation.

Neurons responding to C_2 ganglion stimulation almost never responded to stimulation of other nerves. The cells were not fired by stimulation of the ipsilateral vestibular nerve and also were not excited by stimulation of the deep or superficial radial nerve.

The following experiment as illustrated in Fig. 10 suggests that joint afferents make an important contribution to the pathway. The dorsal neck muscles were removed and bipolar stimulating electrodes were placed both on the region of the atlanto-axial joint and on the C_2 ganglion. Seven neurons were excited by stimulation of the joint area, usually at a latency 0–0.3 ms later than that of the response to ganglion stimulation. The neuron whose response is illustrated in Fig. 10 responded antidromically to floccular stimulation and responded orthodromically to a 7.8V stimulus to the joint area. Following an incision around the stimulating electrodes, the cell did not respond to shocks as strong as 21V.

Figure 11 represents the location of fast green dye marks made after recording from 27 neurons fired by stimulation of the C_2 dorsal root ganglion. Most of the neck relay cells are in the region called group X by Brodal and Pompeiano.[25)] This cell group is known to project to the flocculus. Although there is no anatomical evidence that the external cuneate nucleus projects to the flocculus, some of the marks were clearly in this nucleus.

Discussion

1) *Vestibulo-Neck Reflex*

The pattern of excitatory and inhibitory connections between ampullae and neck motoneurons is quite stereotype (see Fig. 3). The pattern is also consistent with head movements

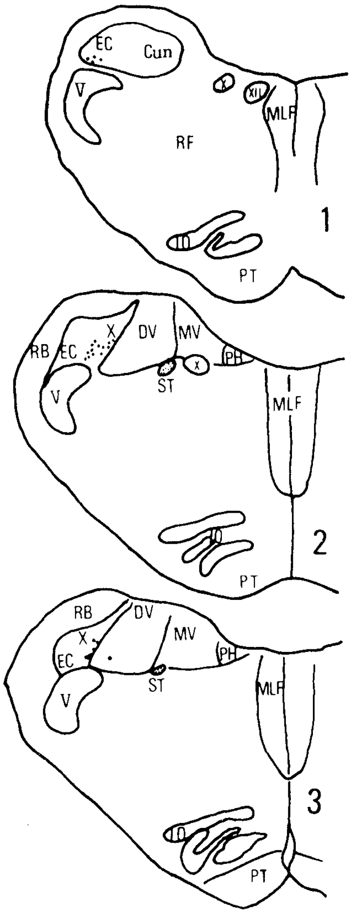

Fig. 11 Location of 23 neurons fired by stimulation of neck afferents. There are three transverse sections numbered 1–3 from caudal to rostral. Abbreviations: Cun, cuneate nucleus; DV, descending vestibular nuclues; EC, external cuneate nucleus; IO, inferior olive; MLF, medial longitudinal fasciculus; MV, medial vestibular nucleus; PH, praepositus hypoglosal nucleus; PT, pyramidal tract; RB, restiform body; RF, reticular formation; ST, solitary tract; x, group x; V, spinal tract of the trigeminal; X, dorsal motor nucleus of the vagus; XII, hypoglosal nucleus.[39]

expected in response to natural stimulation and with those produced by electrical stimulation of the ampullae.[5] The pathway in all cases is disynaptic. Our results reveal the presence of short latency connections between the utricular and saccular maculae and neck motoneurons. In contrast, labyrinthine projections to forelimb motoneurons are weak, and are at least trisynaptic (see Fig. 3), Maeda et al.[20] More generally, there are extensive disynaptic connections between the labyrinth and neck and back motoneurons in cat (Wilson & Yoshida[33] Wilson et al.[34]) and also in frog (Maeda et al.[21]) as well as the pathway of vestibulo-ocular reflex (Baker et al.[1] Highstein et al.[10]). Recent experiments with sinusoidal linear and angular acceleration show that there is a long time phase lag between input acceleration and neck or forelimb muscle responses (K. Ezure, personal communication). This may suggest that pathways more complex than di- or trisynaptic connections must sometimes be important in the production of reflex responses to activation of macular or ampullar receptors.

2) *Cervico-ocular reflex*

With respect to the receptive area responsible for neck-induced motor activities, McCouch et al.[24] stated that it was located in the region of the upper neck joints. The present experiments have shown that abducens motoneurons received inhibition from the contralateral and excitation from the ipsilateral cervical dorsal roots or neck joints. Local application of procaine and circumscribed incision around the stimulating electrode in the joint region abolished the joints-induced effects, indicating that effective volleys may be attributed to those from upper neck joint, probably intervertebrate mechanoreceptors. Magnus[23] and Cohen[6] have suggested that there is an interaction between labyrinthine and cervical influences on motor performance. They stated that the deficits in cats and monkeys caused by cutting or local anesthesia of the C_1 to C_3 dorsal root resemble marked labyrinthine deficit-like disturbances. With respect to cervical influences on the vestibular neurons, anatomical studies (Corbin et al.[7] Brodal et al[4] have shown that cervical afferents project to the vestibular nuclei. Stimulation of the neck joint facilitated the labyrinthine induced IPSP and EPSP in the abducens motoneuron (Fig. 5A). Responses of vestibular neurons to neck joint stimulation were also consistent with the inference derived from the schema in Fig. (Fig. 5C). Bizzi et al.[3] studied eye-head coordination by recording from the neck and eye muscles in monkeys, and they concluded that the head movement provides by way of vestibular and neck proprioceptors the reflex excitation necessary for the compensatory eye movement. The cervico-ocular reflex pathway analyzed here may function cojointly with the vestibulo-ocular reflex to carry the compensatory eye movement.

3) *Neck inputs to the vestibulo-cerebellum*

It has been shown some time ago that the afferents from the upper cervical segments terminate in the caudal brain stem.[7] In the original description, the area of termination of these afferents was not defined, but it was not inconsistent with the location of group X. This cell group is known to receive spinal afferents (Pompeiano & Brodal[25]). The pathway from neck to flocculus via group X is quite specific. Input from neck receptors is ipsilateral and there is no obvious interaction between neck and labyrinthine impulses. This pathway, therefore, differs from the pathway of cervico-ocular reflex described before. The flocculus is involved in eye movement control by its inhibitory action on cells in the vestibular nuclei (Fukuda, et al.[11]), and neck as well as visual information may be required for the proper performance of this control. More information at the unit level is required to understand the proper performance of this control. More information at the unit level is also required for profitable speculation concerning the role of the MF and CF neck information reaching the flocculus and the nodulus.

List of abberviations

Ant (A) : anterior semicircular canal
CF : climbing fiber
DF : dorsal funiculus-
SOCP : spino · olivo · cerebellar pathway
DR : dorsal rami (dorsal neck muscles)
EC : external cuneate nucleus
EPSP : excitatory postsynaptic potential
Hor (H) : horizontal semicircular canal
IO : inferior olive
IPSP : inhibitory postsynaptic potential
LVST : lateral vestibulo-spinal tract
MF : mossy fiber
MLF : medial longitudinal fasciculus
MV : medial vestibular nucleus
PH : praepositus hypoglosal nucleus
POS (P) : posterior semicircular canal
PT : pyramidal tract
RB : restiform body
RF : reticular formation
SP : splenius (dorsal neck muscle)
ST : solitary tract
V : spinal-tract of the trigeminal
VN : vestibular nuclei
X : group X
x : dorsal motor nucleus of the vagus
XII : hypoglosal nucleus

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