Pflügers Arch (1987) 409:13–23

Pflügers Archiv
European Journal of Physiology

Effects of stimulation of vestibular and neck receptors on Deiters neurons projecting to the lumbosacral cord

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Abstract. 1. The activity of lateral vestibular nucleus (LVN) neurons, antidromically identified by stimulation of the spinal cord at T_{12} and L_1, thus projecting to the lumbosacral segments of the spinal cord (lVS neurons), was recorded in precollicular decerebrate cats during rotation about the longitudinal axis either of the whole animal (labyrinth input) or of the body only while the head was kept stationary (neck input). 2. Among the lVS neurons tested for vestibular stimulation, 76 of 129 units (i.e. 58.9%) responded to roll tilt of the animal at the standard parameters of 0.026 Hz, $\pm 10°$. The gain and the sensitivity of the first harmonic responses corresponded on the average to 0.47 ± 0.44, SD, impulses $\cdot s^{-1} \cdot deg^{-1}$ and 3.24 ± 3.15, SD, %/deg, respectively. As to the response patterns, 51 of 76 units (i.e. 67.1%) were excited during side-down and depressed during side-up tilt, whereas 15 (i.e. 19.7%) showed the opposite behavior. In both instances the peak of the responses occurred with an average phase lead of about $+21.0 \pm 27.2$, SD, deg with respect to the extreme side-down or side-up position of the animal. Moreover, the former group of units showed almost a twofold larger gain with respect to the latter group (*t*-test, $p < 0.05$). 3. Among the lVS neurons tested for neck stimulation, 75 of 109 units (68.8%) responded to neck rotation at the standard parameters. The gain and the sensitivity of the first harmonic responses corresponded on the average to 0.49 ± 0.40, SD, impulses $\cdot s^{-1} \cdot deg^{-1}$ and 3.30 ± 3.42, SD, %/deg, respectively, thus being similar to the values obtained for the labyrinth responses. However, 59 of 75 units (i.e. 78.6%) were excited during side-up neck rotation and depressed during side-down neck rotation, while 8 of 75 units (i.e. 10.7%) showed the opposite pattern. In both instances the peak of the responses occurred with an average phase lead of $+52.0 \pm 18.3$, SD, deg for the extreme side-up or side-down neck displacements. Further, the former group of units showed a larger gain than the latter group. 4. Histological controls indicated that 102 of 129 (i.e. 79.0%) lVS neurons tested for labyrinth stimulation and 86 of 109 (i.e. 78.9%) lVS neurons tested for neck stimulation were located in the dorsocaudal part of LVN, the remaining lVS neurons being located in the rostroventral part of LVN. 5. The observation that the predominant response pattern of the lVS neurons to roll tilt was just opposite to that of lVS neurons to neck rotation indicates that the motoneurons innervating ipsilateral hindlimb extensors were excited by an increased discharge of vestibulospinal neurons during side-down tilt but they were disfacilitated by the reduced discharge of vestibulospinal neurons during side-down neck rotation; the opposite would occur during side-up animal tilt or neck rotation. These findings were compared with those of previously recorded LVN neurons, whose descending axons were not identified as projecting to upper or lower segments of the spinal cord. It was then possible to evaluate the role that the LVN exerts not only in the control of the limb but also of the neck extensor musculature.

Key words: Vestibulospinal neurons – Response characteristics – Macular vestibular input – Neck input

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Introduction

Labyrinth and neck afferent volleys elicited either by changing the position of the head with respect to space or the position of the head with respect to the body produce postural adjustments involving the neck and the limb musculature [cf. 26, 39]. In particular, the vestibulospinal reflexes elicited by rotation about the longitudinal axis of the entire animal (roll) or by rotation of the head after neck deafferentation are characterized by excitation of the ipsilateral dorsal neck muscles as the splenius muscle during side-up tilt [3, 6, 40] and the ipsilateral forelimb extensors as the triceps brachii during side-down tilt [5, 18, 23, 28, 31, 40]. For low frequencies of head rotation the peak of these muscle responses was related to position and not to velocity of displacement, thus being attributed to stimulation of macular, utricular receptors. These compensatory vestibulocollic and vestibulo-forelimb reflexes would then operate to maintain the head stationary in the horizontal plane both by righting the head on the neck and by righting the body over the limbs.

As to the cervicospinal reflexes, rotation of the body about the longitudinal axis while maintaining the head stationary or rotation of the head in labyrinthectomized animals causes postural adjustments, characterized by excitation of the splenius muscle during side-down neck rotation, i.e. when chin is rotated maximally contralaterally and by excitation of the triceps brachii during side-up neck rotation, i.e. when chin is rotated maximally ipsilaterally [17, 18, 23, 27, 28, 30, 32]. For low frequencies of neck

rotation the peak of the muscle responses was usually in phase with position. It has been postulated that the cervico-collic and cervico-forelimb reflexes, originally attributed to stimulation of joint receptors [12, 30], are due in part at least to activation of muscle spindle receptors located in the dorsal and the small perivertebral neck muscles [cf. 37, 38].

The postural adjustments produced by vestibular and neck stimulations may involve not only neck and forelimb extensors, but also hindlimb extensors. As to the vestibulospinal reflexes, myographic [11] or electromyographic experiments [4, 29, 36] performed in decerebrate cats have shown that the gastrocnemius-soleus (GS) muscle either did not respond or displayed only small amplitude modulation of its activity to slow roll tilt of the animal or head rotation after neck deafferentation. In these instances the response pattern of the triceps surae to a given labyrinth signal was similar to that of the triceps brachii, although the gain was much smaller; in fact only a limited number of tonically active GS motoneurons [36; cf. also 16], as well as of a primary and secondary endings of GS muscle spindles [11], were excited during side-down head displacement.

As to the cervicospinal reflexes, the triceps surae either did not respond in the same preparations or showed only a small amplitude modulation of its activity suring slow neck rotation. Even in these instances the response pattern of the triceps surae to a given cervical input was similar to that of the triceps brachii, but the gain was smaller [4].

In conclusion, it appears that at least in decerebrate cats the tonic vestibular and neck reflexes acting on hindlimb extensors are negligible or absent, in contrast to those acting on neck and forelimb extensors which are prominent.

The lateral vestibular nucleus (LVN) of Deiters represents one of the main structures which transmits the positional signal from labyrinth and neck receptors to spinal extensor motoneurons. There is in fact evidence that the LVN, which projects ipsilaterally to the whole segments of the spinal cord [35; cf. 33], exerts mono- and polysynaptic excitatory influences on motoneurons innervating hindlimb [20, 21, 24, 42], forelimb [25, 42] and dorsal neck extensors [2, 42]. Moreover, LVN neurons responded to slow rotation about the longitudinal axis of the whole animal [7, 9, 10, 41] or of the neck [8–10] with a periodic modulation of their discharge rate, which was mainly related to the positional signal. Interestingly, a proportion of units were excited during side-down animal tilt and side-up neck rotation, thus having the potential of being involved in the postural adjustments of the limb musculature; however, other units showed the opposite response pattern as expected if they were involved in the vestibular and cervical control of the dorsal neck musculature [7, 8]. In these experiments the recorded units were found to be histologically located within the whole extent of LVN and some of them could also be identified antidromically as vestibulospinal neurons; however, the stimulating electrode was located at high cervical level, so that nothing could be said as to whether the recorded units projected to upper or lower segments of the spinal cord. Moreover, a proportion of LVN neurons were unresponsive to vestibular and/or neck stimulation.

The main aims of the present study were to find out whether in decerebrate preparations the negligible amplitude or absence of modulation of hindlimb extensors to roll tilt of the animal or neck rotation was due to small amplitude or absence of modulation of the corresponding vestibulospinal neurons and, in the former case, whether these neurons responded to the vestibular or neck inputs with a response pattern similar to that predicted for the LVN neurons controlling the limb musculature. For this purpose the activity of vestibulospinal neurons, antidromically identified as projecting to the lumbosacral segments of the spinal cord, was recorded in decerebrate cats and tested during roll tilt of the animal and neck rotation. The results of these experiments were then compared with those obtained in previous experiments [7, 8], in which responses of unidentified units to the same labyrinth and neck inputs were recorded from the whole extent of the LVN which projects not only to the cervical and the lumbosacral enlargements, thus controlling the limb extensor musculature, but also to the upper cervical segments of the spinal cord which control the dorsal neck musculature.

Methods

The experiments were performed in 14 cats (2.5–3.5 kg). Under ether anesthesia the dorsal neck muscles were disconnected bilaterally from the occipital bone and the vertebral axis and partially removed, while the skin of the neck was fully denervated [7, 8, 14, 15]. The axial musculature was also bilaterally disconnected from the dorsal aspect of the vertebral arcs and removed between T_{10} and L_2, to allow exposure of the underlying spinal cord. The animal was then decerebrated at precollicular level, while the cerebellum was left intact.

After interruption of the anesthesia, the head of the animal was placed in a stereotaxic frame and pitched 10° nose-down as in previous studies [7, 8], while the spinous process of the second cervical vertebra was exposed and held by a clamp rigidly secured on a tilting table. In addition, the lower part of the trunk was fixed to a spinal cord frame at T_{11} and L_3 and pins were inserted through the great trochanter of both femurs to prevent body sway. Both fore- and hindlimbs were extended and clamped. Sinusoidal tilting about the longitudinal axis of the whole animal led to selective stimulation of labyrinth receptors; on the other hand, stimulation of neck receptors was performed by tilting the table sinusoidally while the head remained stationary [14, 15]. Rotation at the standard frequency of 0.026 Hz, and at the peak amplitude of displacement of 10° were used.

Three stimulating electrodes made of insulated 200 μm tungsten wire, electrolytically sharpened at the tip and with an interelectrode distance of 1.5 mm, were implanted into the ventrolateral funiculi of both sides as well as along the midline of the spinal cord at T_{12} and L_1.

After these surgical procedures had been performed, the animals were immobilized with pancuronium bromide (Pavulon, Organon, The Netherlands, 0.6 mg $\cdot$ kg^{-1} $\cdot$ h^{-1}, i.v.) and artificially ventilated. At least 2–3 h elapsed in each experiment between the end of the surgical procedures and unit recordings, which allowed a complete recovery of the animal from ether anesthesia.

Neuronal activity was recorded extracellularly with glass microelectrodes (5 to 10 MΩ impedance) filled with a solution of 0.5 M sodium chloride saturated with pontamine blue dye for iontophoretic marking of the recording site.

Rectangular pulses (at 1/s, 0.2 ms in duration, 0.5–10 V) were applied in a unipolar manner between one of the three stimulating spinal cord electrodes (1–10 KΩ impedance) and a reference electrode placed on the body

skin for antidromic activation of LVN neurons. Criteria for identification of antidromic responses including the collision test, and evaluation of the conduction velocity of the corresponding vestibulospinal axons have been previously reported [10]. After application of the antidromic test, the unit activity was selected through a window discriminator and converted to standard pulses. The resting discharge of these neurons was then recorded on magnetic tape and the mean firing rate calculated off line [10]. The unit activity recorded during roll tilt of the animal or neck rotation was processed by a digital signal averager (Correlatron 1024, Laben). Sequential pulse density histograms (SPDHs) with a time base adjusted to cover two full cycles of table movement (128 bins, 0.6 s bin width) were averaged and a Fourier analysis of the unit response was performed following the method described in previous studies [14, 15]. Results are based on the quantitative spectral analysis of the averaged unit activity with respect to the first harmonic of response (output) during the rotational stimuli (angular input).

For each unit, the mean discharge rate or base frequency (impulses/s) was evaluated during animal tilt or neck rotation. For spontaneously active units, this value closely corresponded to the mean firing rate of the same unit recorded at rest. The gain of the first harmonic response was defined as the absolute change of firing rate per degree of displacement (impulses $\cdot$ s^{-1} $\cdot$ deg^{-1}) while the sensitivity expressed the same value as percentage of the base frequency (%/deg). According to the terminology used in previous studies [7, 8, 14, 15] the direction of stimulus orientation was indicated as side-down when rotation of the animal (downward displacement of the table) or of the neck (upward displacement of the table) occurred towards the side of the recording electrode and side-up for rotation in the opposite direction. The phase angle of response corresponded to the phase difference in arc degrees between the peak of the side-down displacement of the animal or the neck and the peak of the fundamental component of unit response. We considered as responsive only those units displaying a stable resting discharge, a reliable modulation of their firing rate during the rotatory stimulus, and a coherence coefficient of the first harmonic to successive cycles of stimulation greater than 0.8; a value of 1.0 represents a linear, time-invariant, noise-free system. In a few instances, units firing at low rate or even silent at rest displayed a cutoff of response during periods of stimulation. These units were used for evaluation of the response gain which was corrected according to the method applied in a previous study [43], but not of the response sensitivity, since in these cases the base frequency represents an overestimate of the resting discharge.

Systemic arterial blood pressure, end-tidal P_{CO_2} and rectal temperature were monitored throughout the experiment and maintained within physiological limits (100–140 mm/Hg, 3–4.5% P_{CO_2}, 37–38° C, respectively). At the end of penetrations a mark was made by passing a cathodal current through the tip of the microelectrode (10–15 μA for 10 min). The method of identifying the location of the recorded units has been described previously [11, 12]. The LVN was subdivided in two parts following the criteria described previously [11, 12]: i) the rostroventral part, rvLVN (sections 1, 2 and the ventral part of sections 3, 4 in Fig. 4), and ii) the dorsocaudal part, dcLVN (sections 5, 6 and the dorsal part of sections 3, 4 of Fig. 4), which project mainly – although not exclusively – to the cervical and the lumbosacral segments of the spinal cord, respectively [35].

Results

Response characteristics of lateral vestibulospinal neurons to sinusoidal vestibular stimulation at standard parameters

The activity of 145 neurons histologically identified as being located within the LVN was recorded and examined during roll tilt of the animal at the standard parameters (0.026 Hz, ± 10°). Among these units, 129 were activated antidromically by electrical stimulation of the spinal cord between T_{12} and L_1; these were therefore considered as lateral vestibulospinal neurons projecting to the lumbosacral segments of the spinal cord (lVS neurons); 110 of these 129 neurons were spontaneously firing at rest. The conduction velocity of the corresponding axons ranged from 33.8 to 124.8 m/s and corresponded on the average to 90.0 ± 21.5, SD, m/s ($n = 129$). The remaining 16 neurons, 14 of which tonically active in the animal at rest, were not antidromically activated by spinal cord stimulation (LVN neurons).

The following data refer to the lVS neurons. In particular, the base frequency evaluated for all the 110 tonically firing lVS neurons (both responsive and unresponsive to tilt), as well as for 8 silent neurons responsive to tilt (see Methods) varied from 0.5 to 70.1 impulses/s corresponding on the average to 24.0 ± 16.9, SD, impulses/s ($n = 118$); its value, however, was lower for the responsive units (20.0 ± 16.2, SD, impulses/s; $n = 76$) than for the units unresponsive to tilt (31.0 ± 15.9, SD, impulses/s; $n = 42$) (t-test, $P < 0.001$). There was a close correspondence between the base frequency of the units tested during animal tilt and the firing rate evaluated for the same units in the animal at rest (resting discharge) (Table 1).

Among the recorded lVS units, 76 (58.9%) responded with a periodic modulation of their discharge frequency in relation to the sinusoidal stimulus. The remaining 53 (41.1%) units did not meet the criteria for responsiveness and were thus considered unaffected by the stimulus.

The gain of the first harmonic response of the lVS neurons to the labyrinth input varied from 0.04 to 2.01 impulses $\cdot$ s^{-1} $\cdot$ deg^{-1}, with a mean value of 0.47 ± 0.44, SD, impulses $\cdot$ s^{-1} $\cdot$ deg^{-1} ($n = 76$), while the sensitivity of the first harmonic response varied from 0.31 to 11.66%/deg, with an average of 3.24 ± 3.15, SD, %/deg ($n = 64$); for the remaining 12 neurons, which were silent or fired at low rate at rest, the sensitivity was not evaluated since the corresponding units showed a cutoff of their responses (Table 1). Histograms of both gain (Fig. 1A) and sensitivity display a rather unimodal long-tailed distribution.

The phase angle of the first harmonic response to standard parameters of tilt was also evaluated and plotted in Fig. 2B. In this histogram, 0° corresponds to the responses displaying a maximal firing rate at the extreme side-down position of the animal and a minimal firing rate at the extreme side-up position, while 180° corresponds to the responses characterized by the reverse pattern. Two main groups of lVS neurons were recognized on the basis of their phase angle distribution. The most prominent group of units (51/76, i.e. 67.1%), which were excited during side-down tilt of the animal, showed a phase angle of responses that ranged from a lead of +75° to a lag of −45°, with an average phase lead of +25.0 ± 23.8, SD, deg (α-responses). The second group of units (15/76, i.e. 19.7%), which were excited during side-up tilt of the animal, showed a phase angle of responses that varied from a lead of +135° to a lag of −105°, with an average phase lag of −172.6 ± 33.9, SD,

Table 1. Response characteristics of antidromic (lVS) and non-antidromic (LVN) neurons to sinusoidal tilt around the longitudinal axis of whole animal (macular input) or rotation of neck (neck input) at standard parameters

	Macular input		Neck input	
	Antidromic	Non-antidromic	Antidromic	Non-antidromic
No of units	129	16	109	13
Responsive (R) units	76 (58.9%) (8 of which silent)	14 (87.5%) (2 of which silent)	75 (68.8%) (5 of which silent)	7 (53.8%) (2 of which silent)
Unresponsive ($\bar{R}$) units	53 (41.1%) (11 of which silent)	2 (12.5%) –	34 (31.2%) (9 of which silent)	6 (46.2%) –
Resting discharge rate of $R+\bar{R}$ units	24.5 ± 15.7 $n = 108$	26.3 ± 15.3 $n = 13$	23.5 ± 16.1 $n = 95$	27.3 ± 16.3 $n = 11$
Resting discharge rate of R-units	21.3 ± 15.4 $n = 68$	26.7 ± 15.9 $n = 12$	21.9 ± 16.5 $n = 70$	23.9 ± 20.8 $n = 5$
Resting discharge rate of $\bar{R}$-units	29.9 ± 14.7 $n = 40$	21.3 $n = 1$	27.8 ± 14.0 $n = 25$	30.2 ± 12.7 $n = 6$
Base frequency of $R+\bar{R}$ units	24.0 ± 16.9 $n = 118$*	23.9 ± 15.9 $n = 16$	23.5 ± 16.8 $n = 100$*	22.2 ± 16.3 $n = 13$
Base frequency of R-units	20.0 ± 16.2 $n = 76$	25.2 ± 16.6 $n = 14$	21.6 ± 17.6 $n = 75$	17.6 ± 20.3 $n = 7$
Base frequency of $\bar{R}$-units	31.0 ± 15.9 $n = 42$*	15.0 ± 6.2 $n = 2$	29.0 ± 12.9 $n = 25$*	27.6 ± 8.9 $n = 6$
Gain of R-units	0.47 ± 0.44 $n = 76$	0.40 ± 0.47 $n = 14$	0.49 ± 0.40 $n = 75$	0.48 ± 0.56 $n = 7$
Sensitivity of R-units	3.24 ± 3.15 $n = 64$	2.00 ± 2.06 $n = 12$	3.30 ± 3.42 $n = 63$	3.08 ± 2.97 $n = 5$
Phase angle of R-units	From $+75°$ lead to $-45°$ lag 51 (67.1%)	8 (57.1%)	From $+90°$ lead to $-15°$ lag 8 (10.7%)	3 (42.9%)
	From $+135°$ lead to $-105°$ lag 15 (19.7%)	4 (28.6%)	From $+165°$ lead to $-90°$ lag 59 (78.6%)	4 (57.1%)
	From $+75°$ to $+135°$ and from $-45°$ to $-105°$ 10 (13.2%)	2 (14.3%)	From $+90°$ to $+165°$ and from $-15°$ to $-90°$ 8 (10.7%)	0

Abbreviations: LVN, lateral vestibular nucleus; antidromic and non-antidromic, LVN units activated or nonactivated antidromically by spinal cord stimulation at $T_{12}-L_1$; resting discharge rate, mean firing rate in impulses/s recorded in the absence of movement; base frequency, mean firing rate in impulses/s evaluated during roll tilt of the animal or neck rotation at standard parameters (0.026 Hz, $\pm 10°$); gain of the first harmonic, change of the mean firing rate per degree of peak displacement (impulses $\cdot s^{-1} \cdot deg^{-1}$); sensitivity of the first harmonic, percentage change of the mean firing rate per degree (%/deg); phase angle of the first harmonic, in degrees of phase lead (positive values) or phase lag (negative values) with respect to the side-down animal or neck displacement.
Values of resting discharge, base frequency, gain and sensitivity are means $\pm$ SD. Figures in parentheses are percentages. The numbers of units used for the evaluation of the base frequency indicated by asterisks are lower than those of the corresponding populations of tested units, due to exclusion of the unresponsive silent units. Moreover, the numbers of units used for sensitivity evaluation of the labyrinh and neck responses were slightly lower than the total numbers of responsive units, since some units that showed a cutoff of their response, either silent or firing at rest, were disregarded; in these instances the cutoff of the unit responses prevented us from taking their base frequency as a reliable indicator of the resting discharge

deg, corresponding to a lead of $+7.4°$ with respect to extreme side-up position (β-responses). In addition to these two populations of units, there were 10 units (i.e. 13.2%) whose phase angle response values were not in the range of the two main populations (intermediate responses) (Table 1).

Fig. 3A represents in a polar diagram both the gain and the phase relation of the responses. Most of the unit responses characterized by an increase in firing rate during side-down tilt (right quadrant) showed a larger gain than that of the units displaying the opposite response pattern (left quadrant).

The results described above were concerned with the first harmonic, which represented the predominant component of responses of the lVS neurons to tilting. A second harmonic was noticeable in most units and had a mean amplitude of 33.7 ± 37.4, SD, expressed in percent of the fundamental ($n = 76$). The response characteristics of the non-antidromic LVN neurons to the same parameters of animal tilt are shown in Table 1.

Localization of units responding to vestibular stimulation

If we consider the localization of all the recorded 145 neurons within Deiters' nucleus, it appears that 34 neurons were located in the rvLVN, while 111 neurons were located in the dcLVN. Moreover, 27 rvLVN and 102 dcLVN units were antidromically identified as lVS neurons (Fig. 4A). Table 2 indicates that the proportion of lVS neurons re-

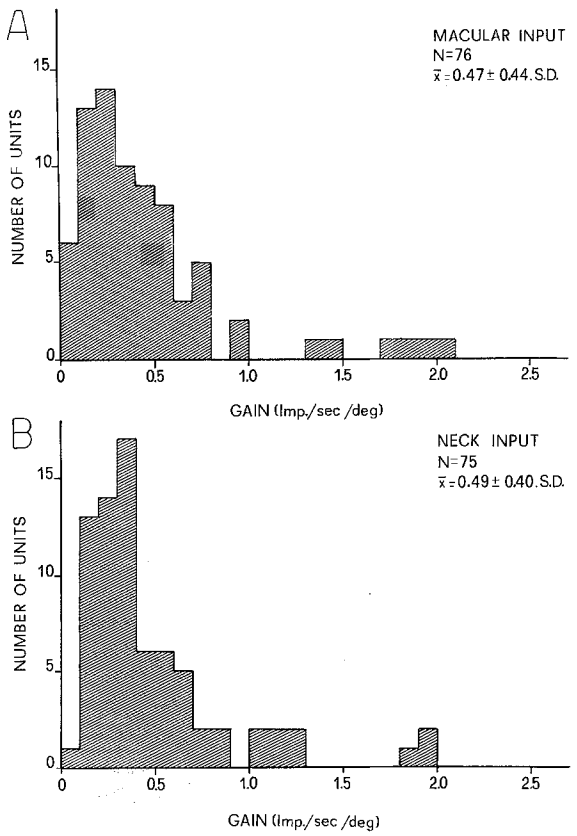

Fig. 1. Gain histograms of the first harmonic of responses of lVS neurons to sinusoidal tilt of the animal (**A**) and neck rotation (**B**) at the standard parameters (0.026 Hz, ± 10°). In particular, 76 LVN units responsive to animal tilt (**A**) and 75 LVN units responsive to neck rotation (**B**) were antidromically activated by stimulation of the spinal cord at $T_{12}-L_1$, thus projecting to the lumbosacral segments of the spinal cord (lVS neurons). Both histograms show a long-tailed unimodal distribution

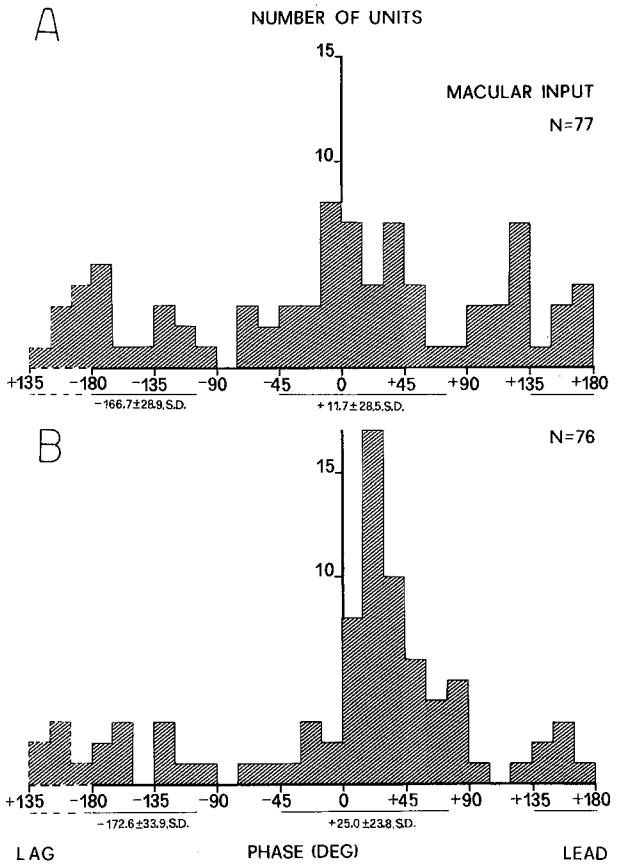

Fig. 2 A, B. Distribution of the phase angle of the first harmonic of responses of different populations of LVN neurons tested during roll tilt of the animal at 0.026 Hz, ± 10°−15°. All the experiments were performed in precollicular decerebrate cats with the cerebellum intact. The upper histogram (**A**) illustrates the distribution of the phase angle of responses to animal tilt of 77 neurons histologically identified as being located within the whole extent of LVN, thus projecting to the whole segments of the spinal cord (slight modified from Fig.3A, Ref. 7), while the lower histogram (**B**) illustrates the distribution of the phase angle of responses to animal tilt of 76 LVN neurons, antidromically activated by stimulation of the spinal cord at $T_{12}-L_1$, thus projecting to the lumbosacral segments of the spinal cord (lVS neurons). Positive numbers in the abscissas indicate in degrees, the phase lead, whereas negative numbers indicate the phase lag of responses with respect to the extreme side-down position of the animal, as indicated by 0°. Responses of the neurons underlined by horizontal bars have been used to evaluate the average phase angle of units excited during, or near the side-down (0°) or side-up displacement of the animal (180°)

sponding to standard parameters of animal tilt was comparable in the rvLVN (17/27, i.e. 63.0%) and the dcLVN (59/102, i.e. 57.8%), as were the average resting discharge rate and base frequency of the two populations of neurons. The gain as well as the sensitivity of the first harmonic responses of the lVS neurons to vestibular stimulation were on the average higher in the rvLVN than in the dcLVN; however, the differences were not statistically significant. Finally, most of the lVS neurons were excited during side-down tilt of the animal; the proportion of units showing this response pattern was higher in the dcLVN (41/59, i.e. 69.5%) than in the rvLVN (10/17, i.e. 58.8%); the difference, however, was not significant.

Response characteristics of lateral vestibulospinal neurons to sinusoidal neck stimulation at standard parameters

The activity of 122 neurons histologically identified as being located within the LVN was recorded and evaluated during neck rotation at the standard parameters. Among these units, 109 were activated antidromically by electrical stimulation of the spinal cord between T_{12} and L_1 (lVS neurons); 95 of 109 neurons were active at rest. The estimated conduction velocity of their axons ranged from 37.1 to 124.8 m/s and corresponded on the average to 89.8 ± 21.0, SD, m/s ($n = 109$). The remaining 13 neurons, 11 of which tonically active in the animal at rest, were not antidromically identified (LVN neurons).

The following data refer to the lVS neurons. The base frequency evaluated for all the 95 tonically firing neurons (both responsive and unresponsive to neck rotation), as well as for 5 silent neurons responsive to neck rotation varied from 0.4 to 68.9 impulses/s, corresponding on the average to 23.5 ± 16.8, SD, impulses/s ($n = 100$); its value was lower for the responsive (21.6 ± 17.6, SD, impulses/s, $n = 75$) than for the unresponsive units (29.0 ± 12.9, SD, impulses/s, $n = 25$); however, the difference was not statistically significant (see Table 1 for the correspondence between mean values of

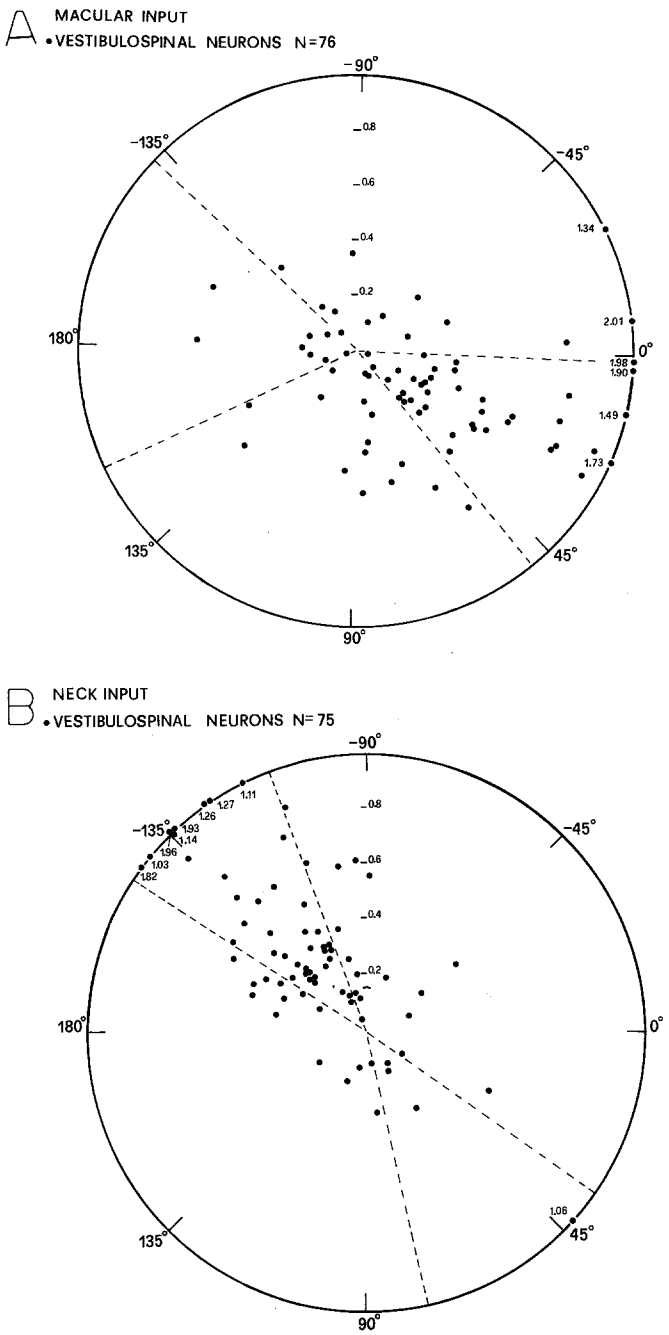

Fig. 3. Polar diagrams showing the gain and the phase angle of the first harmonic of responses of lVS neurons to sinusoidal tilt of the animal (**A**) and neck rotation (**B**) at the standard parameters. The response gain of each unit is indicated by the distance of the corresponding symbol to the center of the diagram (see the scale along the vertical meridian); 6 units in **A** and 9 units in **B** and a gain higher than 1.0. The relative position of the symbol with respect to 0° meridian indicates in degrees the phase lead (positive values) or the phase lag (negative values) of responses with respect to the extreme side-down position of the animal or neck displacement. The dashed lines outline the standard deviation of the phase angle of response of the two main populations of units responsive to animal tilt (**A**) and neck rotation (**B**), as indicated in Figs. 2B and 5B, respectively. In particular, the mean phase angle of the units excited during side-down or side-up animal tilt in **A** corresponded to $+25.0 \pm 23.8$, SD, deg ($n = 51$) and -172.6 ± 33.9, SD, deg ($n = 15$), respectively, while that of the units excited during side-down or side-up neck rotation in **B** corresponded to $+55.9 \pm 21.0$, SD, deg ($n = 8$) and -128.5 ± 18.1, SD, deg ($n = 59$), respectively

base frequency and resting discharge rate of the recorded neurons).

From the total population of recorded lVS units, 75 (68.8%) displayed a periodic modulation of the discharge frequency in relation to the sinusoidal input, while the remaining 34 (31.2%) units did not respond to the stimulus.

The gain of the first harmonic response of the lVS neurons to neck rotation varied from 0.03 to 1.96 impulses $\cdot s^{-1} \cdot deg^{-1}$, with a mean value of 0.49 ± 0.40, SD, impulses $\cdot s^{-1} \cdot deg^{-1}$ ($n = 75$), while the sensitivity of the first harmonic response varied from 0.24 to 13.32%/deg with a mean value of 3.30 ± 3.42, SD, %/deg ($n = 63$); for the remaining 12 neurons the sensitivity was not evaluated, since they were silent or fired at low rate at rest (Table 1). Histograms of both gain (Fig. 1B) and sensitivity display a rather unimodal long-tailed distribution.

The phase angle of the first harmonic response with respect to side-down displacement of the neck was also evaluated. Fig. 5B shows that most of the responsive units (59/75, i.e. 78.6%) were maximally excited by side-up neck displacement (phase angle of responses ranging from a lead of +165° to a lag of −90°), with an average phase lag of -128.5 ± 18.1, SD, deg, corresponding to an average lead of +51.5° with respect to the extreme side-up displacement. On the other hand a smaller group of units (8/75, i.e. 10.7%) were maximally excited by side-down neck displacement (phase angle of responses ranging from a lead of +90° to a lag of −15°), with an average phase lead of $+55.9 \pm 21.0$, SD, deg. Only 8 units (10.7%) fell outside the two ranges reported above (Table 1).

Both the gain and the phase angle of each unit response at the standard parameters of neck rotation were plotted on a polar diagram (Fig. 3B). Most of the unit responses characterized by an increase in firing rate during side-up neck rotation (left quadrant) showed a larger gain than that of the units displaying the opposite response pattern (right quadrant).

In addition to the first harmonic, a second harmonic component of the responses of the lVS neurons to neck rotation was noticeable in most units and had a mean amplitude of 35.2 ± 29.4, SD expressed in percent of the fundamental ($n = 75$). The response characteristics of the non-antidromic LVN neurons to the same parameters of neck rotation are shown in Table 1.

Localization of units responding to neck stimulation

Among all the recorded 122 neurons, 28 were located in the rvLVN, while 94 were located in the dcLVN. Moreover, 23 rvLVN and 86 dcLVN units were antidromically identified as lVS neurons (Fig. 4B). Table 2 shows that the proportion of lVS neurons responding to standard parameters of neck rotation was comparable in the rvLVN (16/23, i.e. 69.6%) and the dcLVN (59/86, i.e. 68.6%), as were the mean resting discharge rate and base frequency of the two populations of neurons. No significant differences in the average gain and sensitivity of the first harmonic of responses to neck rotation were found between the lVS neurons located in the rvLVN and the dcLVN. Finally, most of the lVS neurons were excited during side-up neck displacement; the proportion of units showing this response pattern was slightly higher in the dcLVN (47/59, i.e. 79.6%) than in the rvLVN (12/16, i.e. 75.0%); the difference, however, was not significant.

Fig. 4. Anatomical localization of IVS neurons tested to sinusoidal tilt of the animal (**A**) and neck rotation (**B**) at the standard parameters (0.026 Hz, $\pm 10°$). For each group of experiments the units were plotted on six representative drawings corresponding to transverse sections of the medulla taken at equal intervals and numbered progressively from rostral to caudal levels. The vestibular and cerebellar nuclei were outlined on each of the illustrated sections. Abbreviations: DVN, descending (inferior) vestibular nucleus; *F*, fastigial nucleus; *I*, interpositus nucleus; *LVN*, lateral vestibular nucleus (Deiters); *MVN*, medial vestibular nucleus. **A** Among the 129 LVN neurons antidromically activated by stimulation of the spinal cord at $T_{12}-L_1$ (IVS neurons), 76 units responded to roll tilt of the animal (●), while the remaining 53 units (×) were unaffected by this stimulus. Moreover, 27 of the 129 units (17 of which responsive) were located in the rvLVN while 102 of the 129 units (59 of which responsive) were located in the dcLVN. **B** Among the 109 IVS neurons, 75 units responded to neck rotation (●), while the remaining 34 units (×) were unaffected by this stimulus. Moreover, 23 of 109 units (16 of which responsive) were located in the rvLVN, while 86 of 109 (59 of which responsive) were located in the dcLVN

Comparison of the response patterns of different populations of lateral vestibular neurons to vestibular and neck stimulations

The response characteristics of the antidromic IVS neurons (which project to the lumbosacral segments of the spinal cord), following sinusoidal stimulation of labyrinth and neck receptors, can hardly be compared with those obtained in the present experiments from the non-antidromic LVN neurons (which may actually project to the cervical segments of the spinal cord), since the latter units were few in number and mainly located in the dcLVN. In order to evaluate the responses of lateral vestibular units projecting to different segments of the spinal cord, we should compare the responses of the IVS neurons with those of unidentified LVN neurons, previously tested to vestibular [7] and neck [8] stimulations. In these experiments, in fact, the units were assumed to project to the whole segments of the spinal cord, since they were quite numerous and homogeneously distributed throughout the whole extent of the LVN; moreover, they

Table 2. Localization of antidromic lVS neurons responsive to sinusoidal animal tilt (macular input) or neck rotation (neck input) at standard parameters

	Macular input		Neck input	
	rvLVN	dcLVN	rvLVN	dcLVN
No of units	27	102	23	86
Conduction velocity	93.8 ± 17.4 $n = 27$	89.0 ± 22.5 $n = 102$	92.6 ± 18.6 $n = 23$	89.1 ± 21.6 $n = 86$
Responsive (R) units	17 (63.0%)	59 (57.8%)	16 (69.6%)	59 (68.6%)
Unresponsive ($\bar{R}$) units	10 (37.0%)	43 (42.2%)	7 (30.4%)	27 (31.4%)
Resting discharge rate of R-units	20.6 ± 19.2 $n = 16$	21.5 ± 14.3 $n = 52$	19.8 ± 19.1 $n = 15$	22.5 ± 15.9 $n = 55$
Base frequency of R-units	21.2 ± 19.3 $n = 17$	19.7 ± 15.4 $n = 59$	20.0 ± 19.2 $n = 16$	22.0 ± 17.2 $n = 59$
Gain of R-units	0.59 ± 0.58 $n = 17$	0.44 ± 0.38 $n = 59$	0.58 ± 0.52 $n = 16$	0.46 ± 0.37 $n = 59$
Sensitivity of R-units	4.55 ± 4.17 $n = 14$	2.87 ± 2.74 $n = 50$	4.34 ± 4.56 $n = 12$	3.05 ± 3.10 $n = 51$
Phase angle of R-units	From +75° lead to −45° lag		From +90° lead to −15° lag	
	10 (58.8%)	41 (69.5%)	3 (18.75%)	5 (8.5%)
	From +135° lead to −105° lag		From +165° lead to −90° lag	
	5 (29.4%)	10 (16.9%)	12 (75.0%)	47 (79.65%)
	From +75° to +135° and from −45° to −105°		From +90° to +165° and from −15° to −90°	
	2 (11.8%)	8 (13.6%)	1 (6.25%)	7 (11.85%)

Abbreviations as in Table 1; rvLVN, rostroventral part of LVN; dcLVN, dorsocaudal part of LVN

were not submitted to the antidromic test or else they were antidromically activated by spinal cord stimulation at high cervical level.

Let is consider first the unit responses to vestibular stimulation obtained in the two different groups of experiments. These groups differ first in the proportion of units responsive to sinusoidal tilt of the animal at the standard parameters (0.026 Hz, ± 10°), which was smaller for the antidromically identified lVS neurons (76/129 units, i.e. 58.9%) than for the unidentified LVN neurons (77/102 units, i.e. 75.5%).

As to their response patterns, the neurons recorded in each group of experiments were classified as: 1. units excited during side-down tilt of the animal, with a phase angle of responses ranging from +75° to −45° (α-responses); 2. units excited during side-up tilt of the animal, with a phase angle ranging from +135° to −105° (β-responses), and 3. units showing phase angle of responses outside the range described for the two main populations (intermediate responses). In Fig. 2 the distribution of the response patterns to animal tilt of the identified lVS neurons (B), recorded in the present experiments, is compared with that of the unidentified LVN neurons (A), as recorded in a previous study [7]. Although the majority of the units recorded in both groups of experiments displayed α-responses, their proportion was greater among the lVS neurons (51/76, i.e. 67.1%) than the LVN units (37/77, i.e. 48.0%). Conversely, the proportions of units displaying β- and intermediate responses were smaller among the lVS neurons (15/76, i.e. 19.7% and 10/76, i.e. 13.2%, respectively) than the LVN neurons (20/77, i.e. 26.0% for each group). There are also differences in the average phase angle of responses of the two populations of lVS and LVN units showing α- or β-responses, as shown in Fig. 2. Taken together, the two populations of units showing α- and β-responses displayed an average phase lead with respect to the extreme animal displacements which was larger for the lVS neurons (+21.0 ± 27.2, SD, deg) than for unidentified LVN neurons (+12.3 ± 28.4, SD, deg).

Let us consider now the unit responses to neck stimulation, obtained in the two different groups of experiments. In contrast to the results obtained during animal tilt, the proportion of units responsive to neck rotation at the standard parameters (0.026 Hz, ± 5−10°) was lower for the LVN neurons (70/120, i.e. 58.2%) than for the lVS neurons (75/109, i.e. 68.8%).

As to the response patterns, the neurons were identified as: 1. units excited during side-up neck rotation with a phase angle of responses ranging from +135° or +165° to −90°; 2. units excited during side-down neck rotation with a phase angle ranging from +90° to −15° or −45°, and 3. units showing intermediate responses. Figure 5 compares the distribution of the response patterns to neck rotation of the antidromically activated lVS neurons (B), recorded in the present experiments, with that of the unidentified LVN neurons (A), as recorded in a previous study [8]. The units excited by side-up or side-down neck rotation were almost equally represented among the LVN neurons (38/70, i.e. 54.3% and 31/70, i.e. 44.3%, respectively), while among the lVS neurons there was a predominance of the first population of units with respect to the second one (59/75, i.e. 78.6% and 8/75, i.e. 10.7% respectively). Figure 5 also shows differences in the average phase angle of responses of the

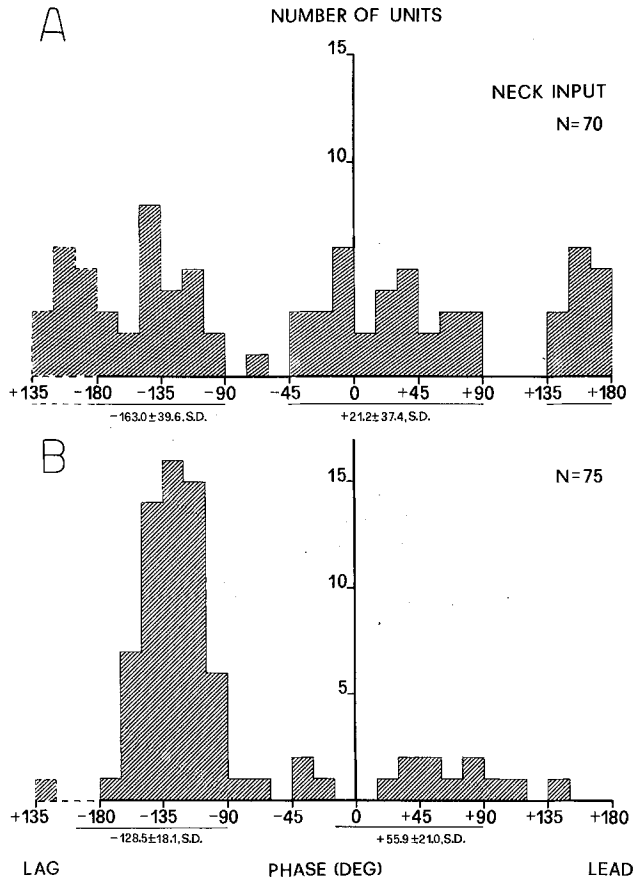

Fig. 5A,B. Distribution of the phase angle of the first harmonic of responses of different populations of LVN neurons tested during neck rotation at 0.026 Hz, $\pm 10°$. All the experiments were performed in precollicular, decerebrate cats, with the cerebellum intact. The upper histogram (**A**) illustrates the distribution of the phase angle of responses to neck rotation of 70 neurons histologically identified as being located within the whole extent of LVN, thus projecting to the whole segments of the spinal cord (slightly modified from Fig. 5A, Ref. 8), while the lower histogram (**B**) illustrates the distribution of the phase angle of responses to neck rotation of 75 LVN neurons antidromically activated by stimulation of the spinal cord at $T_{12}-L_1$, thus projecting to the lumbosacral segments of the spinal cord (lVS neurons). Positive numbers in the abscissas indicate, in degrees, the phase lead, whereas negative numbers indicate the phase lag of responses with respect to the extreme side-down displacement of the neck, as indicated by 0°. Responses of the neurons underlined by horizontal bars have been used to evaluate the average phase angle of units excited during or near side-down (0°) or side-up displacement of the neck (180°)

two populations of lVS and LVN units reported above. Taken together, these two populations of units displayed an average phase lead with respect to the extreme neck displacements, which was larger for the lVS neurons ($+52.0 \pm 18.3$, SD, deg) than for the unidentified LVN neurons ($+18.9 \pm 38.6$, SD, deg).

Discussion

It was previously shown that in decerebrate cats the responses of histologically identified LVN neurons to slow sinusoidal tilt of the animal [7] are mainly related to animal position, thus being attributed to stimulation of macular receptors. Similarly, the responses of LVN neurons to slow neck rotation [8] are related to neck position rather than to velocity of neck displacement, and originate from deep receptors, i.e. joint receptors [12, 30] and/or muscle spindle receptors particularly located in the dorsal and the small perivertebral muscles [cf. 37, 38].

In the experiments reported above [cf. also 34], the proportion of units affected by animal tilt or neck rotation was higher in the rvLVN (91.2% and 73.9%, respectively) than in the dcLVN (67.6% and 48.6%, respectively) which project mainly, although not exclusively, to the cervical and the lumbosacral segments of the spinal cord, respectively [35]. Although the populations of responsive neurons in these two regions of Deiters' nucleus showed a comparable base frequency (43.6 ± 54.4, SD, impulses/s for macular responsive units and 40.7 ± 48.9, SD, impulses/s for neck responsive units), the rvLVN neurons had on the average an higher response sensitivity, but not an higher gain, to both labyrinth and neck inputs with respect to the dcLVN neurons. These differences were attributed to the fact that the primary vestibular afferents from macular receptors as well as the cervical afferents and the related ascending pathways activate more efficiently the rvLVN than the dcLVN.

The rvLVN and dcLVN neurons recorded in the previous studies [7, 8] did not differ with respect to their predominant pattern of response to vestibular stimulation; in fact the proportion of units excited during side-down tilt of the animal (α-responses; 48.0%) was higher than that of the units excited during side-up tilt (β-responses; 26.0%). However, they differ in the distribution of the neck responses; units located in the rvLVN were mainly excited during side-down neck rotation, while most of the units in the dcLVN were excited during side-up neck rotation.

The response patterns characterized by an increase in firing rate during side-down animal tilt and side-up neck rotation have been considered the most appropriate to increase the postural activity in the ipsilateral limb extensors for those directions of animal and neck orientation, while the opposite response patterns have been thought to be quite effective to control the extensor neck musculature (see Introduction). Unfortunately, in the experiments reported above [7, 8] nothing could be said about the precise termination of the vestibulospinal axons originating from the recorded LVN neurons, since the tested units were not identified as projecting to upper or lower segments of the spinal cord.

In the present experiments we recorded the activity of vestibulospinal neurons antidromically activated by stimulation of the spinal cord at $T_{12}-L_1$, thus projecting to the lumbosacral segments (lVS neurons). These neurons were found in both the rvLVN and the dcLVN; however, in our sampled population, the majority of lVS neurons tested to vestibular and neck stimulations were located within the dcLVN (102/129, i.e. 79.0% and 86/109, i.e. 78.9%, respectively).

In spite of the predominant number of antidromic units in the dcLVN, the percentage of lVS neurons responsive to roll tilt of the animal (58.9%) or neck rotation (68.8%) was not significantly different within the two divisions of the nucleus. This finding differs from that previously reported in unidentified LVN neurons, where the proportion of units responsive to standard parameters of animal tilt [7] and neck rotation [8] was higher in the rvLVN than in the dcLVN. Moreover, while the gain and the sensitivity values of all the responsive lVS neurons found in the present study were

on the average similar to those obtained from the whole population of unidentified LVN neurons [cf. also 34], their base frequency evaluated during vestibular stimulation was lower (20.0 ± 16.2, SD against 43.6 ± 54.4, SD, impulses/s); the same was true during neck stimulation (21.6 ± 17.6, SD against 40.7 ± 48.9, SD, impulses/s). Since the unidentified LVN neurons were distributed throughout the whole extent of Deiters' nucleus, thus having the potential of projecting to the whole segments of the spinal cord, our findings indicate that the vestibulospinal neurons projecting to the lower segments of the spinal cord have a mean firing rate lower than that of the units projecting to the upper segments. Moreover, since in the previous experiments [7, 8] no difference in base frequency was found between the two populations of rvLVN and dcLVN neurons, we postulate that at least a proportion of unidentified dcLVN units projected to the cervical rather than to the lumbosacral cord. It appears, therefore, that the whole population of unidentified units histologically located in the dcLVN is less homogeneous than that of the lVS neurons antidromically activated by stimulation of the spinal cord at $T_{12}-L_1$.

In the present experiments the responses of antidromically identified lVS neurons to animal tilt and neck rotation showed on the average phase leads of +21.0° and +52.0°, respectively, with respect to the extreme animal and neck displacements, which contrast with the lower values of +12.3° and +18.9°, respectively, previously obtained from unidentified LVN neurons [7, 8]. Since these last neurons probably included units projecting not only to the lumbosacral but also to the cervical segments of the spinal cord, it is likely that the latter population of neurons showed by itself a smaller phase lead with respect to that obtained from the whole population of unidentified LVN units. This difference can easily be understood if we consider that the majority of recorded lVS neurons were located in the dcLVN and that this part of Deiters' nucleus receives the direct corticocerebellovestibular projection from the anterior vermis [cf. 13], which is inhibitory in function [1, 19, 22]. Since the Purkinje cells of the anterior vermis giving rise to this direct inhibitory projection on Deiters' nucleus actually collaborate with the excitatory macular or neck input in determining the response of the lVS neurons to animal tilt [14] and neck rotation [14, 15], we may assume that the more prominent phase lead of the lVS neurons with respect to those projecting to the cervical segments of the spinal cord is due to corticocerebellar influences acting on these neurons during dynamic stimulation of labyrinth receptors.

A final comment concerns the predominant patterns of responses of the lVS neurons to animal tilt and neck rotation. The majority of responsive lVS neurons displayed an α-response to animal tilt, being excited during side-down tilt of the animal (67.1%; see Fig. 2B); moreover, a great proportion of lVS neurons were excited during side-up neck rotation (78.6%; see Fig. 5B). These proportions were higher than those reported in previous studies (see Fig. 2A and 5A), where the LVN neurons were tested independently upon their axonal distribution [7, 8]. As pointed out previously [cf. 34], these predominant patterns of response are quite appropriate to produce an increased contraction of ipsilateral hindlimb extensors during side-down animal tilt or side-up neck rotation.

Conversely, units excited during side-up tilt of the animal (β-response) and side-down neck rotation were much less represented in our population of lVS neurons (19.7% and 10.7%, respectively) than in the whole population of unidentified LVN neurons [11, 12] (compare Figs. 2B and 5B with Figs. 2A and 5A). It is likely that these two types of unit responses intervene in the control of the dorsal neck muscles, thus being responsible for the increased contraction of the ipsilateral neck extensors during side-up animal tilt or side-down neck rotation [cf. 34]. As to the lVS neurons, which also showed similar response patterns, the most likely hypothesis is that they project either to ipsilateral hindlimb motoneurons different from those controlling the proximal extensor musculature, or to contralateral hindlimb extensor motoneurons [cf. 41]; their activity, however, was apparently weaker than that of the lVS neurons displaying the opposite response patterns.

The demonstration that in decerebrate cats the lVS neurons showing the predominant patterns of response to animal tilt and neck rotation were quite numerous and highly affected by the labyrinth and neck signals contrasts with the fact that in the same preparations the contraction of limb extensor muscles during side-down tilt of the animal and side-up neck rotation involved particularly the triceps brachii, but not the triceps surae [4, 11, 29, 36]. There must be, therefore, other pathways, such as the reticulospinal pathway, which probably contribute with the excitatory vestibulospinal pathway to the postural adjustments during labyrinth and neck stimulations, whose neuronal activity, however, is greatly impaired by the decerebration [cf. 34].

Acknowledgements. This work was supported by National Institute of Neurological and Communicative Disorders and Stroke Research Grant NS 07685-18 and by a grant from the Ministero della Pubblica Istruzione, Roma, Italy. We thank E. Biagetti, U. Corti and Mrs. M. Vaglini for their valuable technical assistance. Dr. A. Marchand was supported by a fellowship of the "Fondation Simone et Cino del Duca, Paris" on leave of absence from the Département de Psychophysiologie générale, Institute de Neurophysiologie et de Psychophysiologie, C.N.R.S., 31 Chemin Joseph-Aiguier, F-13274 Marseille Cédex 2, France.

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Received February 18/Accepted December 10, 1986