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Gravity Responses of Purkinje Cells in the Nodulus

G. Marini, L. Provini and A. Rosina

Laboratorio di Fisiologia dei Centri Nervosi del CNR, Milano (Italy)

Summary. In cats, either decerebrated or under chloralose anaesthesia, Purkinje cells (P-cells) of the cerebellar nodulus have been examined with the animal under static lateral tilt (roll ± 20°). The cell activity was extracellularly recorded and both "simple" and "complex" spike discharge patterns were studied.

In 20 cells out of a population of 198, "simple" spike firing was found to be affected by static roll. Ten cells had an α-type response, 8 a β-type, while only single examples of γ and δ activations were found.

Out of 67 Purkinje cells tested for "complex" spike activation, 5 were found to be sensitive to static roll, 4 with an α or β response and one with a γ response.

The results are to be attributed to pure otolith activation and show that this input is able to modulate P-cell activity in the nodulus through both the mossy fibre and the climbing fibre systems.

Key words: Cerebellum — Otolithic input — Mossy fibres — Climbing fibres.

Introduction

The cerebellum originates from the romboidal lip of the fourth ventricle, a structure which also forms the vestibular nuclei (Larsell, 1923, 1929; Herrick, 1924). This close relationship is maintained in mammals by the vestibular part of the cerebellum (i.e. the flocculo-nodular lobe and the adjoining part of the uvula) which has both direct and indirect input-output relations to the vestibular system (Brodal and Høivik, 1964; Brodal and Torvik, 1957; Angaut and Brodal, 1967; Carpenter *et al.*, 1972). This vestibulo-cerebello-vestibular loop constitutes the morphological basis for the reflex regulation exerted by the vestibulocerebellum on body equilibrium and eye movements, as shown by lesion experiments (Dow, 1938; Carrea and Mettler, 1947; Manni, 1950; Fernandez and Fredrickson, 1964; Grant *et al.*, 1964).

Extensive physiological studies have dealt with the organization of the semicircular canal input to the vestibulocerebellum in conditions of natural stimulation

(Llinás *et al.*, 1971; Precht "unpublished observations", 1974; Shinoda and Yoshida, 1975) and the results have mainly been related to the control exerted by the flocculo-nodular lobe on vestibulo-ocular reflexes (see Ito, 1974).

There is general agreement that the mossy fibre (MF) system carries the vestibular information (Snider, 1936; Brodal and Høivik, 1964; Precht and Llinás, 1969), while more recently it has been shown that natural stimulation of semicircular canals can affect the flocculus also through the climbing fibre (CF) system (Ghelarducci *et al.*, 1975).

The presence of an otolithic component in the primary vestibular input to the flocculo-nodular lobe has been demonstrated on anatomical grounds in the monkey (Carpenter *et al.*, 1972), while there is only indirect evidence that also secondary vestibulocerebellar fibres can carry such an input in mammals (Brodal and Torvik, 1957; Stein and Carpenter, 1967; Gacek, 1969).

The present investigation has been undertaken to determine by means of natural stimulation whether information of macular origin does in fact reach the nodular part of the vestibulocerebellum and to test whether this information reaches the cerebellar cortex through the partecipation of the MF and CF systems. A study of the organization of the otolithic input to the nodulus seems of relevance in view of the fact that knowledge of the afferent connections could help to clarify the reflex regulating function exerted by this part of the vestibulo-cerebellum.

Preliminary reports of these results have already been given (Marini *et al.*, 1975a, 1975b).

Methods

The experiments were performed on 47 adult cats, either decerebrated at precollicular level (25 animals) or under chloralose anaesthesia (22 animals; α-chloralose, 60 mg/kg i.p.). The animals were mounted in a stereotaxic frame and placed on the tilting table with the head 30° downwards. The vertebral column was fixed by rigidly clamping the iliac bones; the thorax and the abdomen were held in place by a special hammock; the fore- and hindlimbs were fixed to the frame in a semi-extended position. A homogeneous white screen, large enough to cover the animal's visual field, was kept in front of the preparation.

The rectal temperature was controlled and kept at 37—38° C by a heating pad or an infrared (I.R.) lamp. A cannula in a femoral artery allowed continuous monitoring of blood pressure.

The cats were paralyzed with periodical injections of gallamine-triethiodide (3—4 mg/kg/h) and artificial ventilation was regulated by monitoring the tidal level of the pCO_2 with an I.R. CO_2 analyzer (Beckman LB-I).

The tilt performed during this study consisted in manually-driven rotations of the animal around its longitudinal axis (roll), to obtain orderly sequences of bilateral stationary positions (from 5° to 20° either side). If tilting induced dynamic effects on the units under study, 5—7 ml of warm (45—50°) and cold (5—10°) saline solutions were injected through eustachian cannulae. To allow this control, during preliminary surgery the eustachian canals were approached from the pharynx and intubated with soft polythene tubing (Ferin *et al.*, 1971).

Glass micropipettes filled with 2 M NaCl (5—10 MΩ) were inserted in a caudo-rostral direction so as to reach lobuli IX and X (uvula and nodulus). During each experimental session one or more pipettes were left "*in situ*" and at the end of the experiment the position of the recorded units was reconstructed histologically by correlating the micropipette tracks with the depth measurements taken from the microdrive during the penetrations (see Fig. 1).

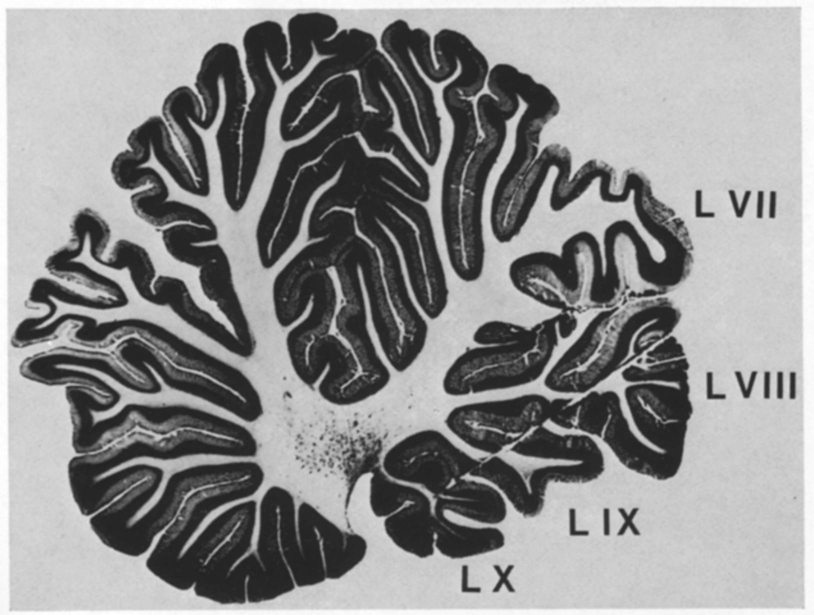

Fig. 1. Sagittal section of the cerebellum showing microelectrode track. The micropipette track directed from the surface of the first folium of lobulus VIII to the uvula (IX) and nodulus (X) can easily be observed

The action potentials were recorded extracellularly with a negative capacitance cathode follower, at unitary gain, fed into an AC preamplifier and displayed on a beam of a Tektronix 565 Oscilloscope. Single spikes were also selected using an amplitude discriminator and converted into square pulses suitable for triggering an integrator (time constant 1 sec). The integrator output was displayed on one channel of a Brush 220 chart recorder giving on-line monitoring of the discharge frequency. Degree of tilt and rate of the movement were continuously recorded by an accelerometer causing DC shifts in a Wheatstone bridge system. The DC level was transferred to the other channel of the chart recorder. Spike activity and tilt position were simultaneously stored on magnetic tape for further analysis. This included basic statistical elaboration by a multichannel analyzer (Mnemotron CAT 400 B).

Results

Identification of Cortical Units under Static Roll

During the present investigation the responses of spontaneously-discharging corticocerebellar units to static roll were studied in detail. The present report relates only to units identified as Purkinje cells (P-cells) by the presence of both "simple" and "complex" spike discharges, reflecting mossy fibre (MF) and climbing fibre (CF) driven activity (Eccles *et al.*, 1967; Thach, 1968). "Simple" and "complex" spike discharges were examined separately.

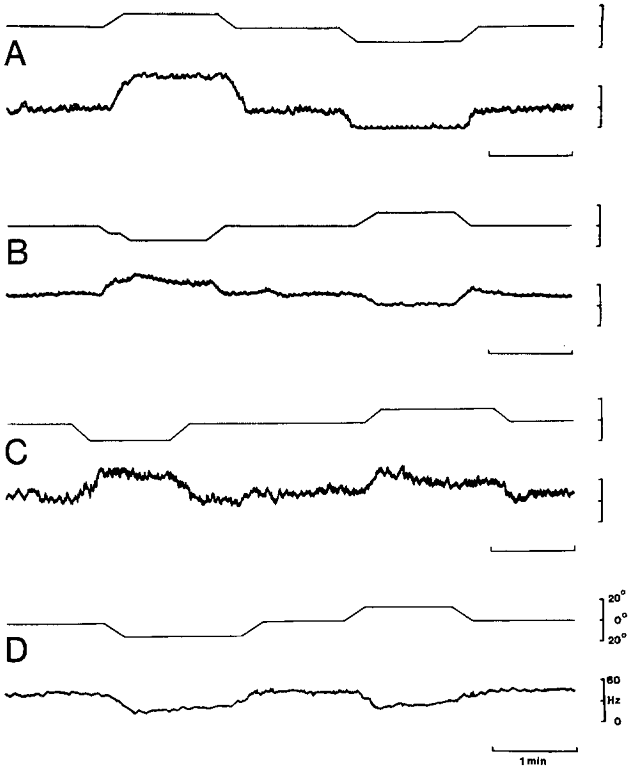

Fig. 2. Discharge rate of P-cells of the nodulus at different degrees of lateral tilt. Upper trace: degrees of lateral roll from the horizontal plane (upward deflection: side down or ipsilateral roll; downward deflection: side up or contralateral roll. Lower trace: mean unitary firing rate. (A) α-type response, (B) β-type response, (C) γ-type response, (D) δ-type response

Table 1. Distribution of tilt-sensitive units according to their response types

Preparation	Tested units	Tilt-sensitive units	Response type			
			α	β	γ	δ
Decerebration . .	124	15 (12.09%)	7 (46.66%)	6 (40.00%)	1 (6.66%)	1 (6.66%)
Chloralose (anaesth.)	74	5 (6.76%)	3 (60.00%)	2 (40.00%)	0	0
Totals	198	20 (10.10%)	10 (50.00%)	8 (40.00%)	1 (5.00%)	1 (5.00%)

Simple Spike Activity of Purkinje Cells

A total of 198 spontaneously discharging P-cells was studied in at least two different roll positions. The resting discharge frequency of simple spike activity of the recorded units varied between 10 and 70 spikes/sec. Of the 198 corticocerebellar units tested, 20 were sensitive to static tilt (10.10%) and their responses are described according to Duensing and Schaefer's nomenclature (1959; see Table 1).

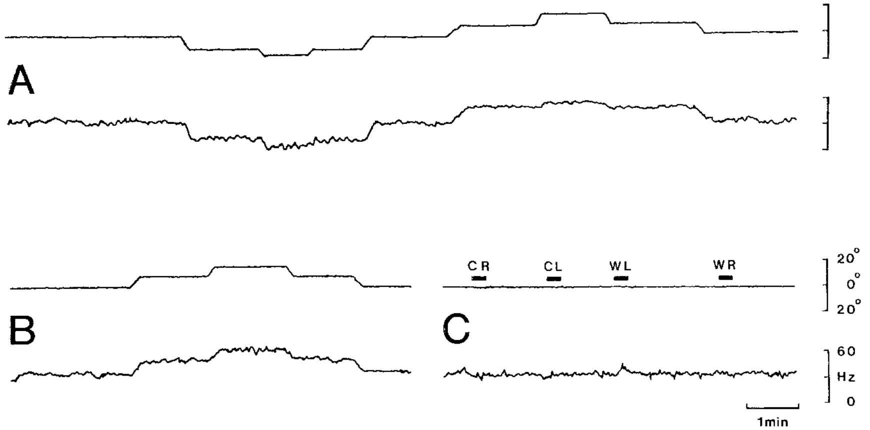

Fig. 3. Discharge rate of a P-cell of the nodulus at several degrees of roll and to labyrinthine caloric stimulation (Plotting conventions as on Fig. 2). The cell firing rate increases during ipsilateral roll and decreases during contralateral roll. There is no response to labyrinthine caloric stimulation (*C* cold Ringer, *W* warm Ringer, *R* right middle ear, *L* left middle ear)

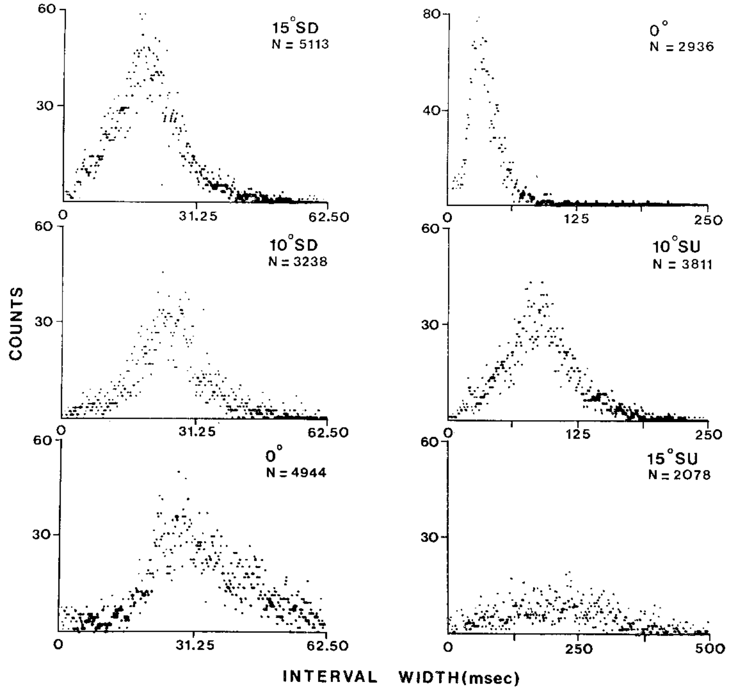

Fig. 4. Interspike interval histograms at different roll positions (this figure is another representation of the data used in Fig. 3). The position from which each histogram was selected is indicated in degrees above each histogram: SD = side down referred to the side of recording, SU = side up referred to the side of recording. The histograms were obtained by a multichannel analyzer CAT 400 B. Note that the number of counts is referred to a 0.156 msec — bin in the histograms in the left row, and to 0.62 msec — and 1.25 msec — bins for the figures on the right

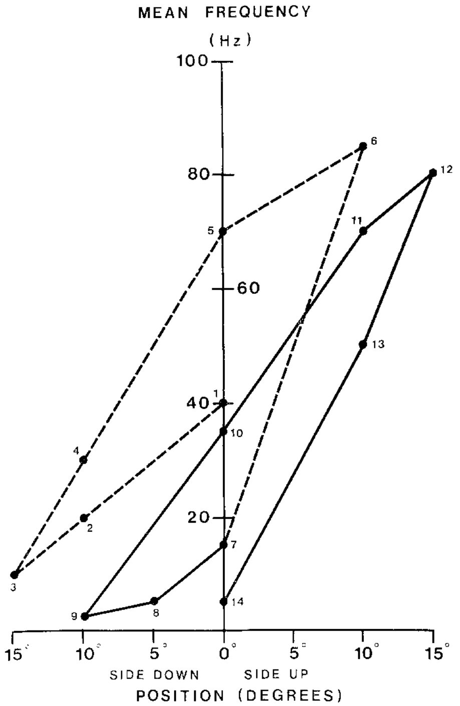

Fig. 5. Relation between mean frequency and roll position. Each point corresponds to a different position: numbers indicate the sequence in the tilt cycle. The position of the head is indicated in degrees between the interaural line and the horizontal plane; side down and side up refer to the side of recording. On the ordinate the mean discharge frequency in spikes/sec, calculated at the steady roll positions. Dashed lines and full lines represent two consecutive tilting cycles of the same unit

It can be seen from the Table that during our study only one γ- and one δ-type responses were found, while α- and β-type responses occurred with the same frequency.

The common response pattern of tilt-sensitive cells (see Fig. 2) consisted of a steady modulation of the discharge rate, lasting as long as the tilt position was maintained. The modulation of the resting discharge frequency could vary up to 350%, a mimimum of 10% for 10° tilt being considered the threshold for a significant response. No obvious quantitative differences were found between the α-, β-, γ- and δ-types of response.

A quantitative relation between angle of tilt and discharge frequency was found even if tilting in opposite directions often yielded asymmetric responses (Figs. 3 and 4). Sequential plotting of the various mean frequencies in the order found during the tilting cycles, revealed aspects which have been described in second-order (Fujita *et al.*, 1968) as well as in first-order (Vidal *et al.*, 1971) vestibular neurons, as "loop" and "creep" figures (Fig. 5).

In few instances, during the first 10—20 sec after a new position was reached, some adaptation occurred (Fig. 2D): the response of macular origin was therefore evaluated on the subsequent steady discharge level (see Discussion). Other units were found to respond with a brief change in mean discharge rate, which lasted no

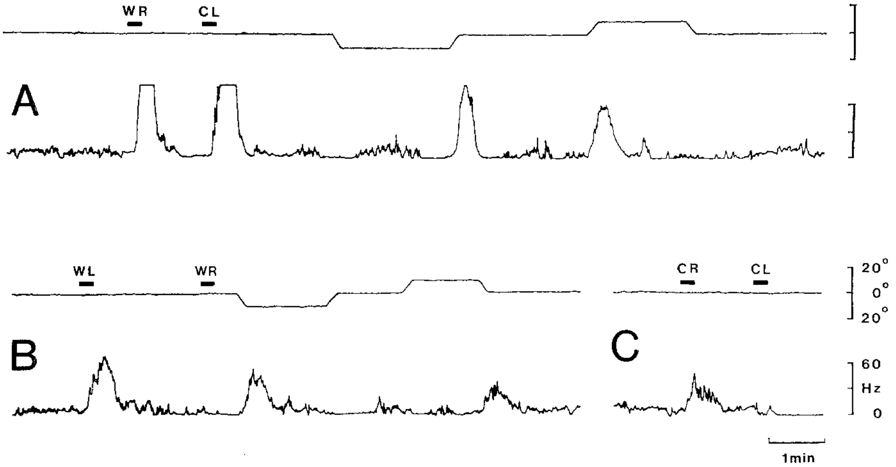

Fig. 6. Activation of P-cells of the nodulus during dynamic phases of tilting and labyrinthine caloric stimulation. The first P-cell (A) is activated by tilting towards the ipsilateral side as well as by irrigation of the right middle ear with warm Ringer (WR) and of the left middle ear with cold Ringer (*CL*). The P-cell illustrated in the lower traces (B, C) is activated by tilting towards the contralateral side as well as by irrigating the left middle ear with warm Ringer (*WL*) and the right middle ear with cold Ringer (*CR*)

longer than the actual displacement and was followed by a return to the frequency level exhibited in the horizontal position. These dynamic responses were seen in 9 of the 74 P-cells in the chloralose anaesthesia preparation (12.18%) and in 6 of the 124 units recorded in the decerebrate preparation (4.83%). A possible ampullary input was then checked (as a control) with caloric stimulation through eustachian irrigation using warm or cold saline solution (Fig. 6).

It was usually found, as shown in the figure, that the effects of caloric stimulation were even stronger than those obtained by moving the animal's head and body. The modulatory effects could be reversed by irrigating the opposite middle ear with the same solution as well as by injecting cold instead of warm saline solution into the same ear (Fig. 6).

Complex Spike Activity of Purkinje Cells in the Nodulus

Out of 67 P-cells having a steady CF-driven activity, 5 (7.46%) were found whose "complex" spike discharge rate was modulated by static roll (two in chloralosed cats and three in decerebrated preparations). Due to the irregular discharge pattern of "complex" spike (see e.g.: Bell and Grimm, 1969), the significance of the discharge modulation was ascertained by the Mann-Whitney U-test (Siegel, 1956) which is independent of the distribution characteristics of the intervals. The null hypothesis was rejected at a 5% confidence limit. The mean discharge rate of the 5 P-cells whose frequency levels were significantly related to tilt positions are plotted in Fig. 7.

It can be seen that 4 of the tilt-sensitive cells showed α- or β-type sensitivity, while one of these exhibited γ-type responsiveness.

The "simple" spike discharge had a regular pattern in only 39 of the cells tested for CF activation and in none of them showed a significant modulation after

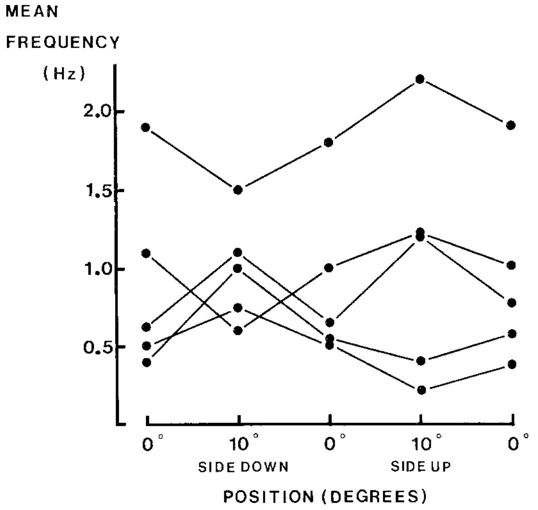

Fig. 7. Complex spike activity of five P-cells of the nodulus during lateral tilt. The mean discharge frequency has been plotted in horizontal position (0°), with the side of recording tilted downward and tilted upward. As it can be seen, two P-cells have α-type and two β-type responses. One cell shows a γ-type activation. The modulation of the discharge rate is significant ($P < 0.05$, Mann-Whitney U-test)

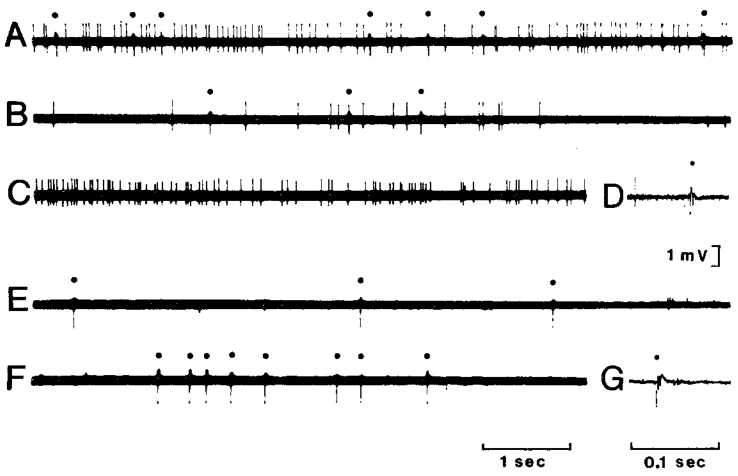

Fig. 8. Examples of P-cells whose "complex" spike discharge was significantly (U-test; $P < 0.05$) modulated by otolith afferences. The cell illustrated in A—D had an incostant "simple" spike discharge while complex spike discharge decreased from A (ipsilateral side down 10°), B (0°) to C (ipsilateral side up 10°). The cell E-F-G was sensitive only to caloric stimulation and did not exhibit "simple" spike discharge. Time calibration of G applies also to D

tilting. In no P-cell were we able to ascertain a modulation of the "complex" spike activity during the dynamic phase of tilt: on the contrary it was not unusual to induce a short burst of "complex" spikes in a P-cell during labyrinthine caloric stimulation (Fig. 8).

Discussion

This study shows that P-cell activity in the cerebellar nodulus can be modulated by static lateral tilt, that is by macular activation. Actually under our experimental conditions stimulation of extramacular receptors — such as visual or neck receptors — had to be excluded (see Methods).

May we remind that the firing rate modulation which took place during the displacement of the table and during the first 20 sec after a new position had been reached, was evaluated separately from the steady activity (Fujita *et al.*, 1968; Peterson, 1970) since it could be referred to the ampullary activation of vertical canals, and/or to a possible dynamic component of the macular responses (Schor, 1974).

Simple Spike Activity of Purkinje Cells

About 10% of the P-cells examined showed a clear modulation of the discharge rate to static roll. The incidence of units sensitive to lateral tilt is similar to that found in other nervous structures where the macular input has been studied using this same natural stimulation. Sensitive units were in fact 9 and 14% respectively in the medullary and pontine reticular formations (Spyer *et al.*, 1974), 19% in the precerebellar reticular nuclei (Ghelarducci *et al.*, 1974) and 22% in the rostral part of the fastigial nucleus (Ghelarducci, 1973).

A higher percentage (35%) of P-cells in the flocculus is modulated by semicircular canal afferences (Ghelarducci *et al.*, 1975). This discrepancy can be explained on the one hand by the fact that primary vestibular afferents have a greater projection to the flocculus than to the nodulus (Carpenter *et al.*, 1972) and on the other hand by the different experimental situations. In our preparations, in fact, a large amount of tonic cerebellar afferences which could be coactivated during tilting was eliminated through gallamine intrafusal and extrafusal blockade as well as through decerebration or chloralose anaesthesia.

According to our results the bulk of the activation pattern is represented by α and β responses which are the response types found in both first-order (Vidal *et al.*, 1971; Fernandez *et al.*, 1972) and second-order vestibular neurons (Fujita *et al.*, 1968; Peterson, 1970). These findings are in agreement with the anatomical data showing that both primary and secondary vestibular fibres reach the vestibulocerebellum (Snider, 1936; Brodal and Høivik, 1964).

The respective contributions of primary and secondary vestibular afferents could not be ascertained in our study. It must be considered, however, that in the nodulus the same proportion of α and β responses was found to occur, while it is well known that in both vestibular nerve and vestibular nuclei neurons the α-type response represents the more frequent response pattern (Peterson, 1970; Vidal *et al.*, 1971; Fernandez *et al.*, 1972). This sort of redistribution of α and β responses can be explained taking into account that, while primary vestibulocerebellar fibres have an almost homolateral projection, the secondary vestibular afferents have bilateral connections (Brodal and Høivik, 1964; Brodal and Torvik, 1957; Carpenter *et al.*, 1972). In this way an α response carried by the contralateral afferent would be recognized as a β response at the nodular level.

The presence of γ and δ responses in the nodulus can be referred to the convergence of ipsi- and contralateral otolithic inputs carrying α or β responses. In this respect the partecipation of polysynaptic vestibulocerebellar pathways involving the main reticular formation as well as the precerebellar reticular nuclei should also be taken into account (Spyer *et al.*, 1974; Ghelarducci *et al.*, 1974).

The different degrees of activation of these polysynaptic vestibulocerebellar pathways might in part explain the different amount of tilt-sensitive units found in our two experimental situations — i.e. chloralose anaesthesia and decerebration (see Table), since it has been shown that the information transfer across the cerebellar glomeruli — i.e. the MF-granule cell synapse — is conditioned to a great extent by the activity of the reticular system (Allen *et al.*, 1972; Gordon *et al.*, 1972; Azzena and Ohno, 1973).

In no case we found a clear ampullary-macular convergence on a single P-cell. This would indicate that the utricular afferents reach a specific population of nodular P-cells: a finding which is in agreement with anatomical data (Carpenter *et al.*, 1972). It should be pointed out, however, that the ampullary stimulation we used was weak and limited and therefore no definite conclusion can here be drawn.

Complex Spike Activity of Purkinje Cells

In this study some P-cells were found to respond to static roll with a modulation of "complex" spike discharge. These results give the direct evidence that natural stimulation of the otolith organs is capable of activating the CF pathway to the vestibulocerebellum. The possibility that natural vestibular stimulation could also activate the CF system was supported by an earlier observation made during caloric or galvanic stimulation of the labyrinth (Ferin *et al.*, 1971). Experimental evidence has recently been produced that CF modulation can also be obtained in the flocculus following natural activation of the semicircular canals (Ghelarducci *et al.*, 1975).

In view of the fact that anatomical evidence for a direct vestibular projection to the inferior olive is lacking (Walberg, 1956; Weiss *et al.*, 1964; see however Brodal, 1974), our results can only be explained by postulating a multisynaptic pathway, as already suggested by Precht and Llinás (1969) on the basis of electrical stimulation of the vestibular nerve. Among the numerous structures which might be involved in the decerebrate preparation, one should mention the main reticular formation and the precerebellar reticular nuclei, where the presence of tilt-sensitive cells has been demonstrated (Spyer *et al.*, 1974; Ghelarducci *et al.*, 1974). On anatomical grounds other structures such as the dentate nucleus (Carpenter *et al.*, 1972; Graybiel *et al.*, 1973), the nucleus interpositus of Cajal and the periacqueductal grey (Carpenter and Hanna, 1962; Carpenter and Strominger, 1965) should also be considered.

The absence of tilt-sensitive cells in the inferior olive (Ghelarducci *et al.*, 1974) can be related to the small incidence of tilt-responses (7.47%) found in our study; to say nothing of the possibility of extraolivary sources of climbing fibres (Sasaki *et al.*, 1969; Batini and Pumain, 1971; Rivera-Domiguez, 1974).

The present results also show an example of tonic modulation of CF-driven discharges, such as the one found in the vermis during the different phases of sleep (Marchesi and Strata, 1970; Mano, 1970; Hobson and McCarley, 1974).

The finding that otolithic afferences reach the cerebellar nodulus through both MF and CF systems supports the view that these systems cooperate in carrying this same sensory information to the nodular cortex. However the lack of MF and CF convergence onto the same P-cell seems to favour the possibility that in natural operating conditions afferences from other receptors such as those of the neck (Wilson *et al.*, 1975) and/or visual ones (Maekawa and Simpson, 1973) converge on the same cerebellar unit, there to allow an integration with the vestibular information. A good example of such convergence has recently been provided by Ghelarducci *et al.* (1975) in the floccular part of the vestibulocerebellum.

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Dr. G. Marini
Dr. L. Provini
Dr. A. Rosina
Laboratorio di Fisiologia
dei Centri Nervosi del C.N.R.
Via Mario Bianco, 9
I - 20131 Milano
Italy