

ELECTROPHYSIOLOGICAL STUDY ON COLLICULO-CEREBELLAR PATHWAY IN CAT

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ABSTRACT

The retino-colliculo-cerebellar and visual cortical-cerebellar pathways were re-examined by means of latency measurement of evoked potentials on 50 immobilized cats.

1. The vermician cerebellar response to optic nerve stimulation was a large positive wave sometimes superimposed by small waves in the decay phase. The positive wave was considered to originate from the mossy fiber system, based on the results obtained from the relation of this wave to evoked spike responses recorded from the deeper layers.
2. The latencies of cerebellar, collicular and visual cortical responses to optic nerve stimulation were 6.3-7.5, 3.5-4.0, and 5.3-7.3 msec, respectively. The latency of the cerebellar response to visual cortical stimulation was 6.0-6.9 msec, while that of the collicular response to visual cortical stimulation was 1.5-2.0 msec.
3. Two positive waves (C_1 and C_2) were evoked in the cerebellum by superior colliculus stimulation. The latencies of these waves were 1.5-2.5 and 3.5-4.3 msec, respectively. C_1 was evoked by stimulation of any layer of the superior colliculus, while C_2 was evoked by stimulation of only the optic and intermediate layers. A striking property of C_2 was its very delayed recovery, in contrast to C_1 .

The present results indicate that C_1 has a definite relation to the retino-colliculo-cerebellar route and C_2 related to the route from visual cortex to cerebellum, and lead us to reconfirm that the main pathway carrying visual information to the cerebellum was relayed at the superior colliculus.

INTRODUCTION

Since the precise analysis made by Fatiga et al.¹⁾ (1959) of the pontine responses to optic nerve stimulation in the cat, the colliculo-ponto-cerebellar pathway has commonly been accepted as the main route carrying visual information to the cerebellum, first asserted by Snider and Stowell²⁾ (1944) and Snider³⁾ (1945). However, exact morphological evidences have not been obtained that the colliculo-cerebellar pathway is mediated through the pontine nuclei. The route from the visual cortex to the cerebellum, established by Dow⁴⁾ (1942), Jansen and Fangel⁵⁾ (1961), Deura⁶⁾ (1961) and Munson⁷⁾ (1968), has not been morphologically substantiated. Recently, Maekawa and Simpson⁸⁾ (1973), based on results obtained

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from the climbing fiber responses in the flocculus of the rabbit cerebellum, reported that the optico-cerebellar projection passed through the pretectum and the inferior olive. Supporting their results, Mizuno et al.⁹⁾ (1974) proved morphologically the pretecto-olivary connections. Graybiel¹⁰⁾ (1974), by applying the orthodromic and antidromic autoradiographic trace technique on rat and cat brains, found that the ventral part of the lateral geniculate body also sent fibers to the cerebellum via the pontine gray.

These new results on the routes of visual inflow to the cerebellum led the author to re-examine the colliculo-cerebellar relation in the cat, by the method of latency measurement of evoked responses, and the findings showed that there were two collicular efferent fiber groups to the vermian cerebellum.

METHODS

Experiments were performed on 50 cats of both sexes weighing 2.5-3.5 kg. The animal was anesthetized with ethyl ether for tracheotomy and trachea cannulation, through which artificial respiration was performed during the experiments, and was immobilized with flaxedil (gallamine triethiodide, 20-30 mg) intravenously administered through the radial vein. Then, the head was fixed to a stereotaxic instrument under local anesthesia of pressure points with 2% lidocaine hydrochloride (TEI-SAN). The visual cortex of both sides and the posterior of the cerebellum were exposed. Care was taken to prevent drying of the brain surface by covering with a thin layer of 0.8% agar-physiological solution. To keep the body temperature near normal, the animal was placed on a hot-pack. An additional dose of 10 mg of flaxedil was sometimes given as required for maintenance of immobilization. Most experiments took 7 to 10 hours.

Evoked potentials were recorded by silver ball electrodes of 250 μm in diameter from the surface of the cerebellum and the visual cortex. Indifferent electrodes were embedded into the muscle behind the ear. Extracellular spike discharges of cerebellar neurons were also recorded with Pt-Ir microelectrodes having a tip diameter of about 10 μm and impedance of 40 to 100 Kohms at 1 KHz, or glass micropipettes filled with 3 M NaCl having the resistance of about 8 Mohms. To stimulate the optic nerve, two Pt-Ir wires of 200 μm in diameter, each of which was insulated with glass except for the tip, were used, as a bipolar electrode, with the inter-electrode distance of 200 μm . These were placed on the optic disc after removing the cornea, the lens and the vitreous body of the globe. Through this electrode the rectangular electrical pulses were given with the duration of 0.1-0.2 msec, but the intensities were altered from 5 to 40 volts as required. Another bipolar electrode was also prepared for the collicular stimulation. This consisted of two silver wires of 100 μm in diameter, each of which was insulated with Araldite (CIBA GEIGY) except for the tip and mounted together in the injection needle with an inside diameter of 250 μm . The distance between the two silver wires was about 200 μm . This bipolar electrode was used also for the recording the collicular evoked re-

sponses. In some cases, photic stimulation was carried out by means of diffuse illumination with a duration of 150-300 msec, and frequency of 0.2-0.4 c/s, using a projector lamp positioned 150 cm away from the eyes, and when there were 300 lux. at the eye. Sometimes, a small spot (10 cm in diameter) stimulation with a luminance of about 300 lux. was projected on a screen 50 cm in front of the eye.

Unit activities were also recorded from the cerebellar cortex through a cathode follower preamplifier having the time constant of 0.003 sec. After the experiment, the brain was perfused with a 10 % formalin solution applied through the radial vein. The fixed tissue served as histological preparations for identification of position of the electrode tip. These preparations were stained with Hematoxylin-Eosin or Luxol First Blue.

RESULTS

1. Cerebellar evoked responses to optic nerve stimulation

The wave forms and the latencies of cerebellar responses elicited by optic nerve stimulation were observed in the first series of experiments. The evoked responses were five times superimposingly recorded from several points, separated 2 to 3 mm, at the pial surface of each folia of tuber vermis, pyramis, uvula, bilateral lobuli paracentralis and hemispheres around the vermis. A typical data of mapping carried out by these means are illustrated in Fig. 1. The opticocerebellar responses were obtainable from the surface of the posterior vermis and from the middle folia of the lobuli paracentralis, and were particularly in high amplitude at three loci, that is, the central area of the tuber vermis, the flexive portion and the caudal portion of the pyramis. No responses were recorded from the marginal area of the lobuli paracentralis, nor from the cerebellar hemispheres. To obtain the maximum amplitude from the posterior lobe of the vermis, the stimulus intensities should be about 30 volts, with the stimulus duration fixed at 0.2 msec. The amplitude reached about 1 mV. and a small negative wave was often preceded by the large positive wave. Three positive wavelettes were sometimes superimposed on the decay phase. The latencies of these responses varied without any topographical order in different portions. No relation was found between the latency and the response amplitude so that shorter latencies were not always obtained from the response of higher amplitude (Fig. 1). In this experiment, therefore, responses from the central area of the tuber vermis were taken as a standard of latency measurement, because this area was the most easily accessible and central in the topographical distribution of evoked responses. The latencies obtained from several experiments, were in the range of 6.3 to 7.5 msec (mean: 6.5 msec), and the peak latencies were 8.0 to 10.0 msec.

The responses from the cerebellar cortical depth in the same area were recorded to analyse the origin of these responses. At a depth of 50 μ m from the surface, two positive waves were obtained. The first wave was always reliably evoked but the second one was not (Fig. 2). When the electrode was further advanced, the first wave increased gradually up to its maximum amplitude at the depth of about

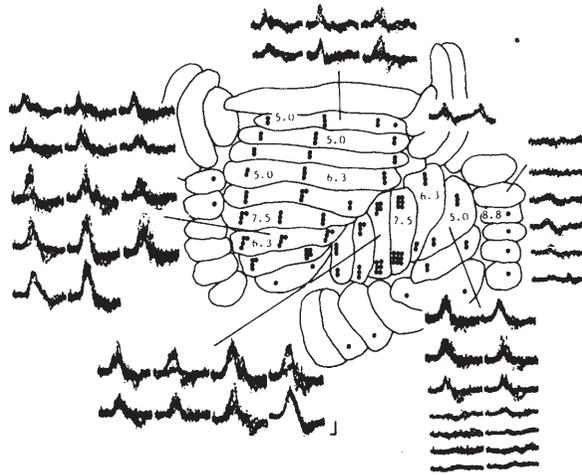


Fig. 1. Distribution of the evoked potentials and their latencies at cerebellar posterior lobe by optic nerve stimulation (intensity, 30 volts, duration, 0.2 msec). This schema indicates that there is no relation between amplitude, latency and distribution. Upward deflection indicates positivity in this and all subsequent figures. One black circle, 100 μV . Number, latency (msec). Vertical bar, 100 μV . Horizontal bar, 5 msec.

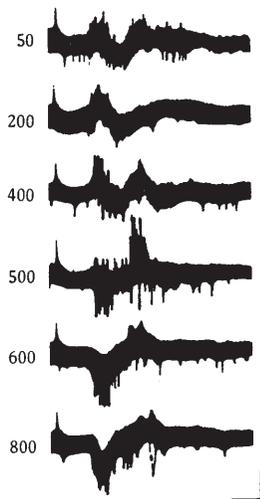


Fig. 2. Changes of intracortical evoked responses at cerebellar tuber vermis following optic nerve stimulation. The first responses show that field potentials at 500 μm from the surface are inverted from positive to negative waves upon which spike discharges are superimposed. On the second responses, the large spike discharges are superimposed. Number, the depth from cortical surface (μm). Vertical bar, 100 μV . Horizontal bar, 5 msec.

200 μm and then decreased gradually to reverse its polarity to negative at around 500 μm . This wave was considered to have the same origin with that of the surface response because of the same latencies. The second one reached maximum at 400 to 500 μm , the latency of the arising phase being 14.0 ± 1.0 msec. During advancement of the electrode from 200 to 600 μm , the spike discharges initially appeared

superimposed on the first wave and at around 500 μm depth, another large spike activity appeared on the second wave. The depth of 400 μm corresponded to the Purkinje cell layer (Eccles et al.¹¹1967).

Next, the responses of the visual cortex and the superior colliculus to optic nerve stimulation were recorded simultaneously with the cerebellar responses and these were compared in the same preparations (Fig. 3). The contralateral collicular responses to the stimulated side were recorded at every 1 mm step during electrode advancement after the collicular surface was reached.

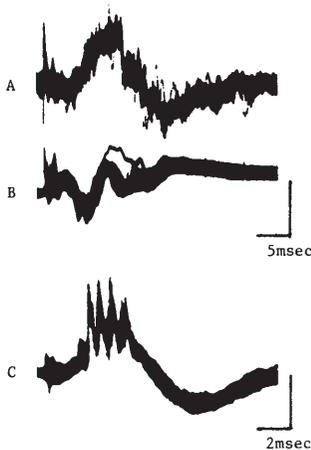


Fig. 3. Optic nerve stimulation. Recording sites; A: cerebellum (tuber vermis). B: visual cortex (posterior suprasylvian gyrus) contralateral to the stimulated side. C: superior colliculus (optic layer) contralateral to the stimulated side. Vertical bar, 200 μV .

The level of the surface was determined by the aid of an audiometer and by a small response with an additional short step. As a preliminary experiment, the depth of the electrode tip was identified in the histological preparation. The site producing the largest responses consisting of repeated waves was obtained in the level of the optic layer as described by many researchers (Marchiafava and Pepeu,¹² 1966). In such a typical response, the latency of the arising phase of the first positive wave in the polyphasic response was from 3.5 to 4.0 msec.

The visual cortical responses were recorded from the surface of the posterior suprasylvian gyrus contralateral to the stimulated side, which has been considered as the region connected with cerebellar activities. These appeared as negative-positive diphasic waves and the latency of the first descending phase ranged from 5.3 to 7.0 msec.

2. Cerebellar evoked responses to superior colliculus stimulation

The collicular responses to optic nerve stimulation were at first recorded at each depth as mentioned above, and in each step, stimulus was applied through the recording electrode. The cerebellar surface responses to superior collicular stimula-

tion were obtained at each step as shown in Fig. 4. The response initially consisted of a positive wave having the peak latency of about 3.0 msec, but when the stimulus electrode was further advanced, the response doubled, that is, a second positive wave with the peak latency of about 6.0 msec appeared following the first wave.

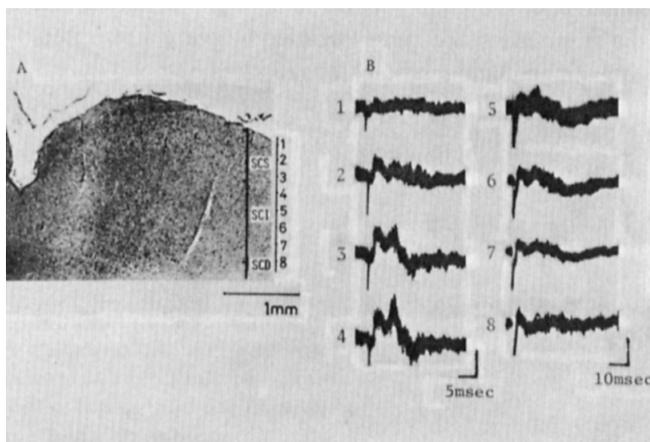


Fig. 4. Cerebellar evoked responses to intracollicular stimulation. A: photomicrograph of coronal section through the colliculus showing electrode track. SCS, Strata grisea colliculi superioris. SCI, Strata grisea colliculi intermediale. SCD, Strata grisea colliculi profundum. B: cerebellar response to intracollicular stimulation at each number portion as shown in A. Maximal cerebellar responses were evoked by stimulation at 4 (intermediate gray layer).

This stimulated layer probably corresponded with the intermediate layer (Snider and Niemer,¹³ 1964), because it was met after passing through the optic layer described above. With the stimulus electrode fixed at this layer, the cerebellar response was observed. Two waves were called C_1 and C_2 in order of latency. To obtain their maximum amplitude, the intensity of 35 volts with the duration of 0.2 msec was necessary. The threshold of C_1 was lower than C_2 . (Fig. 5). In the cerebellar cortex, the recording electrode was advanced deeper into the Purkinje cell layer, after recording C_1 and C_2 . At this layer, the early negative-positive complex (n_1) and the late negative wave (n_2) appeared distinctly with the stimulus of 30 to 40 volts (Fig. 6). The latencies, the peak latencies and the intensity-amplitude curve of these waves showed a good correspondence with those of the surface responses. The latency, thus measured, ranged from 1.5 to 2.5 msec for C_1 and from 3.5 to 4.3 msec for C_2 .

To analyse the difference between C_1 and C_2 , recovery of these waves was observed by means of double stimulation. Both test and conditioning stimuli were constantly 30 volts and 0.2 msec, but the interstimulus interval was altered from

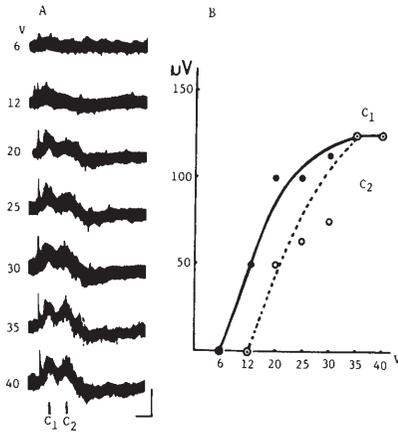


Fig. 5. Intensity-amplitude curves of cerebellar waves evoked by superior colliculus stimulation. A: cerebellar evoked response to collicular stimulation at intermediate layer. B: intensity-amplitude curves given from the evoked responses in A. C₁ and C₂ were positive waves. Number, stimulus intensity (volts). Vertical bar, 100 μ V. Horizontal bar, 2 msec.

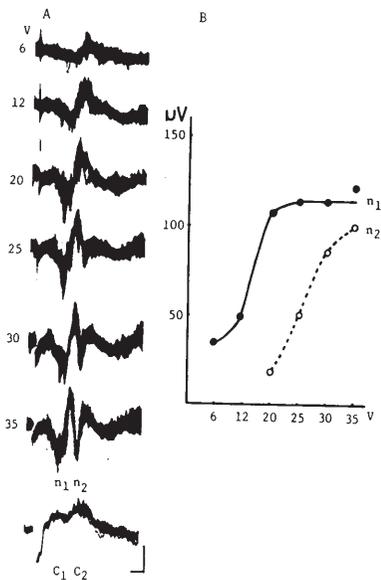


Fig. 6. Intensity-amplitude curves of evoked waves at Purkinje cell layer to collicular stimulation. A: n₁ and n₂ are negative waves of the evoked responses at Purkinje cell layer, following collicular stimulation at the intermediate layer. Note correspondance of the negative waves with the surface positive waves. Number, stimulus intensity (volts). Vertical bar, 2 msec. B: intensity-amplitude curves of two negative waves in A.

10 to 900 msec (Fig. 7). There was a depression of both C₁ and C₂ when the interval was about 15 msec. At the interval of more than 15 msec, C₁ appeared fully with almost the same amplitude as that by conditioning stimulus, while C₂ showed a refractoriness more than 20 msec. The C₂ was again significantly suppressed during a period of about 40 msec to 400 msec after the conditioning shock. Such a peculiar property might suggest complicated underlying mechanisms distinguishing it from C₁.

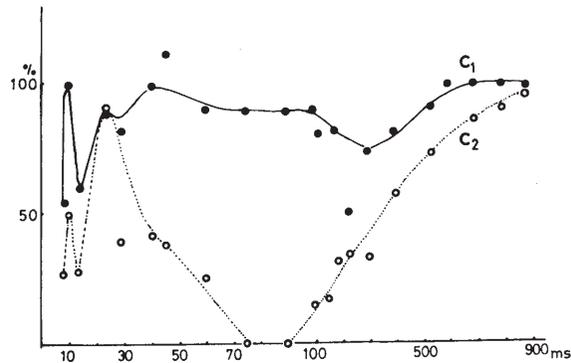


Fig. 7. Recovery curves of cerebellar waves evoked by collicular double stimulation. Ordinate: percentage of positive waves (C_1 and C_2) evoked by test stimulus to ones following conditioning stimulus. Abscissa: stimulus-interval of double stimulation. Recovery curve of C_1 shows relatively constant recovery after 15 msec of interval except for the dip at about 200 msec, an inhibition of recovery from 80 to 100 msec and gradual recovery from 150 msec.

3. Cerebellar responses to visual cortical stimulation

With stimulation of the posterior suprasylvian gyrus, the largest response was recorded from the intermediate layer of the colliculus as shown at C in Fig. 8, which was employed for effective stimulation site to produce C_1 and C_2 . The cerebellar surface responses were also recorded simultaneously (A in Fig. 8), and

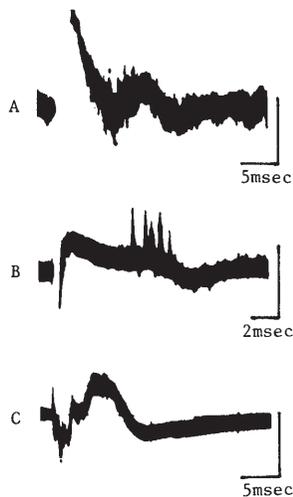


Fig. 8. Visual cortical stimulation. Recording sites: cerebellar evoked response (A, tuber vermis), cerebellar evoked spike discharges (B) to visual cortical stimulation, and superior collicular response (C). Vertical bar, 200 μV in A and C, 1 mV in B.

more B in Fig. 8. shows unit discharges to stimulation of the same portion. The collicular responses were polyphasic and the cerebellar one was a monophasic wave. The latencies were 1.5 to 2.0 msec and 6.0 msec respectively.

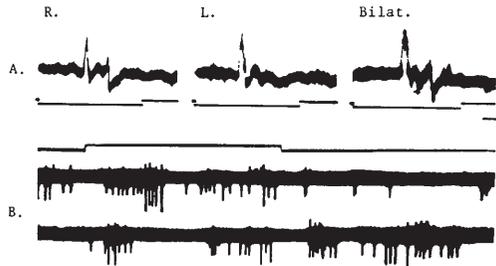


Fig. 9. Cerebellar evoked response to photic stimulation. A: diffuse photic stimulation to right eye (R), left (L) and bilateral eyes (Bilat). Lower rectangular pulse wave, 100 msec of duration of photic stimulation. Vertical bar, 100 μ V. Horizontal bar, 20 msec. B: Changes of cerebellar spike discharges to repetitive spot light illumination on the screen in front of both eyes. Upper rectangular wave, 300 msec. Vertical bar, 500 μ V.

Response	SC	VC	CBL	
	Evoked Pot.	Evoked Pot.	Evoked Pot.	Spike Dis.
ON	3.5-4.0	5.3-7.0	6.3-7.5	6.5-11.3
	4.0-5.0 (Marchiafava & Pepeu)	6.0-7.0 (Malis & Kruger)	7.0-10.0 (Buchtel et al.)	
SC		No response	1.5-2.5 (C ₁) 3.5-4.3 (C ₂)	
VC	1.5-2.0		6.0-6.9	5.3-7.3
	0.8-2.5 (Hoffmann & Straschill)		8.0-12.0 (Snider & Eldred) 6.0 (Deura)	

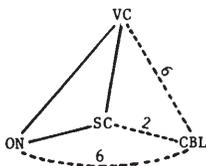


Table 1. latencies of visual centers and vermian cerebellum to optic nerve, superior colliculus and visual stimulations. Stim, stimulating portion. ON, optic nerve. SC, superior colliculus. VC, visual cortex. Response, responding portion. CBL, cerebellum (tuber vermis). Pot, potential. Dis, discharge. Number, latency (msec). Lower schema shows approximate latency at each visual center.

4. Cerebellar responses to light stimulation

With diffuse illumination, a train of positive waves were recorded from the surface of the posterior vermis (Fig. 9A). Whichever eye was stimulated, the responses were almost the same, and when both eyes were stimulated, the effect seemed to be summated. Corresponding with these waves, the Purkinje cell discharges were also recorded, but these were sometimes masked by spontaneous discharges (Fig. 9B). A spot projected on the screen did not stably elicit the responses. Only occasional responses occurred. The latencies were generally 30 to 40 msec with maximum stimulus intensities.

Table 1 sums up the latencies of the evoked responses obtained, particularly in reference to the visual pathways to the cerebellum, and compares them with the results described by other researchers.

DISCUSSION

Regarding the wave forms, latencies and distribution of cerebellar responses elicited by optic nerve stimulation, the present results were almost similar to those observed by Snider and Stowell (1944), Fadiga et al.¹⁴⁾ (1957), Koella¹⁵⁾ (1959), and Buchtel et al.¹⁶⁾ (1972). As summarized in Table 1, latencies of the responses at many visual centers were also comparable with those of previous works by Snider and Eldred¹⁷⁾ (1951), Malis and Kruger¹⁸⁾ (1956), Deura (1961), Marchiafava and Pepeu (1966), Hoffmann and Straschill¹⁹⁾ (1971), and Buchtel et al. (1972), respectively. The slight difference between each experiment and individual deviation of measurement may be due to the characteristics of cerebellar activities influenced by multiple and combined sensory inputs, as already pointed out (Dow and Moruzzi,²⁰⁾ 1958 and Brookhart et al.,²¹⁾ 1950). Therefore, the systematic latency measurement seemed to be valuable for a general consideration of opticocerebellar pathways.

The large positive waves recorded from the cerebellar surface evoked by optic nerve stimulation are considered as relating to the mossy fiber inputs for the following reasons. These waves showed a similar time course with the first waves recorded from the deeper layer. The responses from this depth are the mossy fiber responses as identified by Buchtel et al. (1972) by their analysis of unit activities and also by Kwan and Murphy²²⁾ (1974) by their laminal analysis. Further, the second waves recorded from the deep layer are considered to be climbing fiber responses, because the time course and the recording site are identical to those obtained by Buchtel et al. The comparison of latencies between cerebellar, collicular and visual cortical responses recorded simultaneously, demonstrates that the large positive waves from the cerebellar surface may have no connection with the input from the visual cortical responses. In contrast to these waves, small positive wavelettes on their decay

phase may originate from this retino-visual cortico-cerebellar pathway because of their longer latencies. From these findings, the total conduction time from the optic nerve through the visual cortex to the cerebellum should be more than 13 msec. Thus, the present results support the validity of the description that visual information to the cerebellum is mainly via the retino-colliculo-cerebellar route cited by many researchers (Snider and Stowell, 1944, Fadiga et al.,²³⁾ 1959).

The C_1 of cerebellar responses to collicular stimulation seemed to be the mossy fiber origin. The sum of the latency of C_1 and that of collicular response to optic nerve stimulation nearly equals the latency of the large positive response in the cerebellum elicited by optic nerve stimulation. As the mossy fibers originate from the pontine nuclei (Eccles, Ito, Szentagotai, 1967), the latency measurement of C_1 supports the evidence that the colliculo-cerebellar pathway is relayed at the pontine nuclei (Crosby,²⁴⁾ 1962). It is still unclear morphologically, however, whether the collicular fibers relay in the pontine nuclei. There are also results in the early step, by Ogawa and Mitomo²⁵⁾ (1938) and Larsell²⁶⁾ (1943) suggesting the existence of direct colliculo-cerebellar routes. There has not been found any description on this C_2 . The considerably long latency and the characteristic property induced by double stimulation clearly suggest that C_2 is elicited by the volley mediated through polysynaptic connections. Although small unmyelinated colliculo-cerebellar fibers described by Jansen and Brodal²⁷⁾ (1954) may be considered to have a relation to this long latency of C_2 , the present data is not sufficient to evaluate this problem. The addition (7.0-8.3 msec) of the latency of collicular response to optic nerve stimulation and that of C_2 , on other hand, were not so long as that of the climbing fiber responses (14 ± 1.0 msec), which were obtained from the cerebellar deep layer when the optic nerve was stimulated, nor long enough as those (17-20 msec) described by Buchtel et al. (1972). Rather, the C_2 occurred within the period of the first wave obtained from the cerebellar deep layer. The sum of the latency of collicular response to visual cortical stimulation and that of C_2 is seemingly identical with the latency of cerebellar response to visual cortical stimulation. Further, C_2 was maximally evoked when the intermediate layer of the colliculus was stimulated, where the descending fibers from the suprasylvian gyrus terminate (Crosby, 1962). These results may indicate that C_2 has some relation to the pathway from the visual cortex to the cerebellum.

It was especially noticed that under diffuse or spot photic stimulation, the slow response from pial surface and spike activities were both unstable, being influenced by the background activities. Visual control of cerebellar activity may not be predominant among those of several sensory modalities, at least, in the cat.

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