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The Effect of Pentothal on the Activity Evoked in the Cerebellar Cortex

M. Gordon*, F. J. Rubia** and P. Strata
Istituto di Fisiologia dell'Università di Pisa and Laboratorio di Neurofisiologia del CNR, Pisa (Italy)

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Summary. In precollicular decerebrate cats, limb nerves have been stimulated and field potentials and unitary activity recorded from the cerebellar cortex. Doses of pentothal up to 8 mg/kg affect neither the activity evoked in the fast mossy fibre pathways, nor the size of the postsynaptic potentials in granule cells, but the axon discharge in these latter cells is clearly affected. With 4—8 mg/kg the axon discharge of granule cells is abolished and as a consequence Purkinje cells do not respond to the peripheral stimulation via the mossy fibres. In contrast the activity evoked through the climbing fibres is enhanced. This effect takes place at precerebellar level. Both the effects on the mossy fibre and climbing fibre pathways show a recovery in 15—60 min depending on the dose.

Key words: Cerebellum — Barbiturates — Unitary activity

Introduction

A series of recent investigations have provided a detailed picture of the wiring diagram of the cerebellar cortex and of the pattern of activation of its elements under the influence of the mossy fibre (MF) and the climbing fibre (CF) inputs (Eccles, Ito and Szentágothai, 1967). It has been shown that this pattern may be modified by anaesthesia (Bloedel and Roberts, 1969; Eccles, Faber and Táboříková, 1971). It has been recently reported that barbiturates depress activity evoked by the MF input (Körlin and Larson, 1970; Eccles, Faber, Murphy, Sabah and Táboříková, 1971 b), but the place of the action is not known. Nothing has so far been reported on the activity evoked by the CFs. Concerning the spontaneous activity of the Purkinje cells small doses of pentothal have a depressive action (Murphy and Sabah, 1970). This effect if marked on the MF driven spikes and weaker on the CF driven spikes (Latham and Paul, 1971).

The present experiments are aimed at describing how the pattern of activation of the cerebellar cortex by a peripheral stimulus is modified as a function of barbiturate anaesthesia. The understanding of such a modification is important in order to better evaluate the significance of results obtained in different experimental conditions.

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* Postgraduate student of the Scuola Normale Superiore of Pisa.

** From the Physiological Institute of the University of Munich, West Germany. Supported by the Deutsche Forschungsgemeinschaft.

Some of these results have been published as brief communications (Gordon *et al.*, 1972a, 1972b).

Methods

The experiments were performed on 14 adult cats. Under ether anaesthesia several limb nerves of the left side were dissected and prepared for later placing on bipolar silver stimulating electrodes. These nerves usually were the superficial radial, the tibial and the sural. The animals were then decerebrated at precollicular level following ligation of both carotid arteries. The preparation was fixed in a stereotaxic apparatus and the nerves placed on the stimulating electrodes and then covered in a pool of warm paraffin oil. Under continuous irrigation of Ringer solution the anterior lobe of the cerebellum was exposed by removing the bony tentorium. In some animals transfolial (TF) and juxtafastigial (JF) electrodes were implanted in the cerebellum (Eccles, Sasaki and Strata, 1967), which was then covered with a 2% Agar solution in Ringer. Limb nerves were stimulated once every second with square pulses of 0.025—0.05 msec duration and with amplitudes of 1.5—6 times the threshold. Recordings in the cerebellar cortex of the left anterior lobe were made by using glass micropipettes with a resistance of 2—10 MΩ. The field potentials recorded in this way were fed into a cathode follower, filtered with a time constant of 100 msec, then amplified through a Tektronix 2A63 amplifier and displayed on a 565 Tektronix oscilloscope. The activity was also routinely fed into a computer (Enhancetron ND 800) for averaging. The averaged activity was then written with an X—Y plotter. Unitary activity was recorded on film with a Grass camera directly from the cathode ray oscilloscope. The identification of the field potentials as due to MF or CF inputs was based mainly on the criterion of the latency and also of the pattern as described previously (Eccles *et al.*, 1968a; Buchtel *et al.*, 1972).

Intravenous injection of pentothal (Farmotal: sodium 5-etyl-5-(1 methylbutyl) 2-thiobarbiturate, Farmitalia) was done several times in the same experiment. With doses of 4—8 mg/kg the usual interval between two successive trials was at least 1 hour.

Results

1. Field Potentials Generated by a Nerve Volley in the Unanaesthetized Decerebrate Cat

Stimulation of a limb nerve in the unanaesthetized decerebrate cat evokes in the cerebellar cortex field potentials, which differ strikingly from those obtained in intact nembutalized animals. The fields obtained in the latter condition have been fully described in a previous paper (Eccles *et al.*, 1968a). The major difference in our experimental conditions concerns the depth profile of the field evoked through the MF afferents, as illustrated in Fig. 1. This profile is very similar to that obtained in the vermal visual area of the intact unanaesthetized cat by electric shock stimulation of the optic nerve or the superior colliculus and by a flash of light on the retinae (Buchtel *et al.*, 1972). In the molecular layer (A, B and C) there is mainly a large N_3 wave, which is preceded by a small positivity corresponding to the reversal of the N_2 wave of the granular layer. In the latter layer the N_2 wave is followed by a sharp P_2 wave and a prolonged negativity.

A profile like that illustrated in Fig. 1 can be interpreted as due exclusively to the activation of the MF afferents. Although seldom appearing in the nembutalized animal, this profile has been very frequently encountered in our decerebrate preparations. Moreover, a later component, identified as due to the CF afferents, has also been found in association with the MF component, but rarely alone. This latter observation has been made very frequently in the nembutalized animal. Examples of fields evoked through both MF and CF afferents are illustrated in Fig. 2.

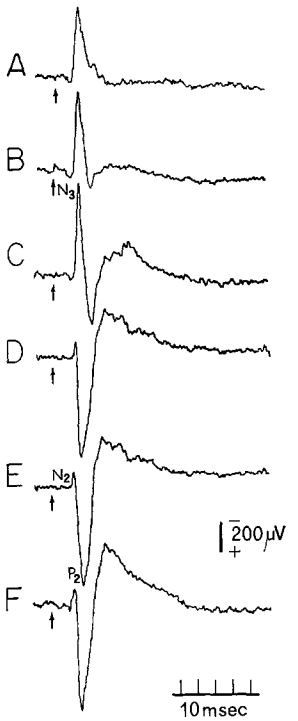

Fig. 1. *Depth profile recorded from the cerebellar cortex following stimulation of a limb nerve in the unanaesthetized decerebrate cat.* The arrows indicate the time of application of an electrical stimulus, 1.5 times the threshold, to the tibial nerve. The responses are evoked by the mossy fibre input. Each specimen is the average of 25 responses. The different specimens were taken by moving the microelectrode in 100 μ steps

In conclusion, the main difference between the fields described previously in the nembutalized cat and in the present unanaesthetized decerebrate preparation is that in the latter condition the MF input seems to be more powerful in activating the cerebellar cortex, a finding confirming the observation given in a previous paper concerned with unitary activity (Eccles *et al.*, 1971 b).

2. The Effect of Pentothal on the Responses Evoked in the Cerebellar Cortex by a Limb Nerve Volley

A relatively small dose of pentothal (0.5—8 mg/kg) has been tested on the different patterns of fields evoked by a single shock applied to forelimb or hindlimb nerves. Some fields were apparently evoked exclusively through the MF afferents, some through the CF afferents and some through both. These fields were recorded either in molecular or in granular layers. Concerning the MF evoked fields, after the intravenous injection of 4—8 mg/kg of pentothal, the N_2 wave in the granular layer and the positivity preceeding the N_3 wave in the molecular layer did not show an appreciable change, whereas there was a complete or an almost complete suppression of the P_2 and N_3 waves and the subsequent negativity. In contrast, the CF evoked activity, represented by the later negative or

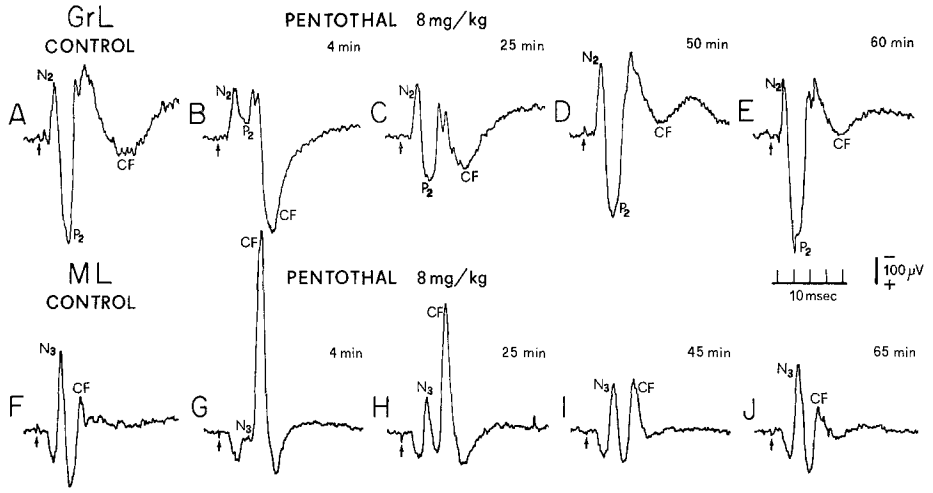

Fig. 2. *The action of pentothal on the field potentials evoked by limb nerve stimulation.* In A there is a response evoked in a granular layer (GrL) of the cerebellar cortex in a decerebrate unanaesthetized cat following stimulation of the tibial nerve. The N_2—P_2 waves of the mossy fibre input and the late wave due to the climbing fibre input (CF) have been labelled. B—E illustrate the effect of the intravenous injection of 8 mg/kg of pentothal after 4, 25, 50 and 60 min respectively. F—J illustrate the same phenomenon in a molecular layer (ML). Every specimen is the average of 50 responses

positive wave recorded respectively in molecular and granular layers, showed an earlier peak and a larger amplitude. These effects were fully reversible in about 15 to 60 min depending on the dose of pentothal used.

Figure 2 shows two fields recorded respectively from the granular layer (GrL) and from the molecular layer (ML) of the lobulus IV of the anterior lobe in a decerebrate unanaesthetized cat. The fields in A and F evoked by stimulation of the tibial nerve, consist typically of an early and a late component. In A, the early component shows N_2—P_2 waves followed by a large negativity, the N_2 having a latency of 7 msec. This pattern corresponds to the component generated through the fast MF pathways as described in the previous paragraph. The late positive component, indicated by CF, having a latency of 25 msec and interrupting the MF evoked field, corresponds to the wave generated by the activation of the CF afferents. The record of B, taken 5 min following the intravenous pentothal injection, shows that an 8 mg/kg dose does not alter remarkably the size of the N_2 wave, which shows a decrease of only 10%, whereas the large P_2 and the later large negative wave are almost completely suppressed. In contrast the CF field undergoes a striking increase in size and reaches its peak earlier. The records of C, D and E show the same field taken respectively 25, 50 and 60 min after the pentothal injection, and show a gradual recovery, which can be considered complete in the last record.

In this same experiment, after the recovery took place, the electrode was advanced a few microns and the activity of a Purkinje cell was recorded. With a slight further advancement there was the field illustrated in Fig. 2F—J. The

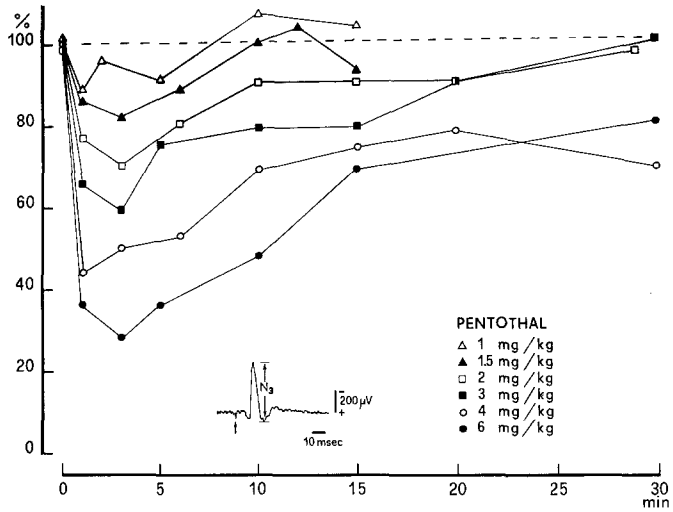

Fig. 3. *The effect of different doses of pentothal on the mossy fibre response evoked in the cerebellar cortex by stimulation of the tibial nerve.* The size of the N_3 wave in the molecular layer has been measured before (control) and after the intravenous injection of different doses of pentothal. The reduction of the N_3 wave has been plotted as a percentage of the control at different time intervals. The specimen is the average of 25 control responses (N_3 wave) recorded in the molecular layer. The interval between two successive pentothal injections was 30 min for doses up to 2 mg/kg and 60 min for higher doses

electrode was probably in the molecular layer corresponding to the granular layer illustrated in Fig. 2A—E. The two layers were separated by a distance of less than 300 μ. Figure 2F shows that the same stimulus applied to the tibial nerve evokes a positive wave, which is the reversal of the N_2 wave recorded in the granular layer and a large N_3 wave followed by a positivity. A later CF evoked field is rather small and difficult to identify. G shows that following the intravenous injection of 8 mg/kg of pentothal the early positive wave remains almost unaltered, whereas the N_3 is almost completely suppressed. In contrast a clear CF field appears with a remarkable size. The records of H, I and J taken respectively 25, 45 and 65 min after the pentothal injection show a gradual recovery, which appears to be completed in J. The increase in the CF fields is not present consistently in all the single evoked responses, which are characterized by a large variability in size.

The threshold dose of pentothal which affects both MF and CF fields is around 0.5—1 mg/kg. Figure 3 illustrates in one experiment the effect on the N_3 wave of different doses of pentothal and shows a dose of 1 mg/kg affecting the transmission in the MF pathway. In other experiments 0.5 mg/kg gave a reduction of the N_3 or P_2 waves up to 30% relative to the control.

Often the CF evoked field was not detectable in the unanaesthetized state and it appeared only after the injection of a small dose of pentothal. One example has been illustrated in a previous paper (Gordon *et al.*, 1972b, Fig. 1).

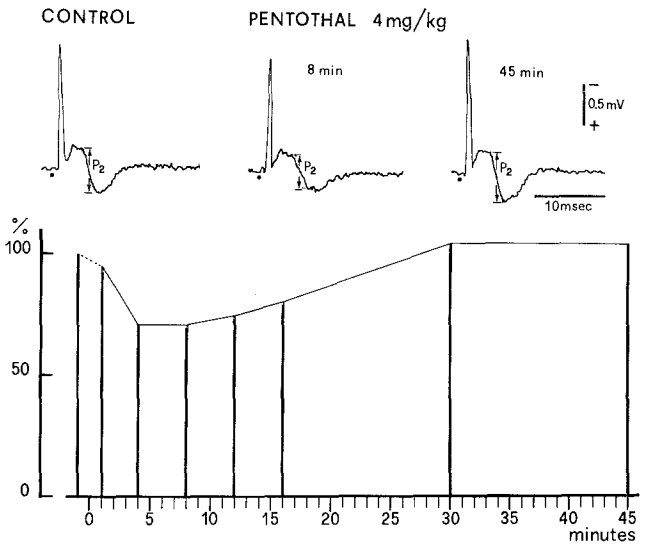

Fig. 4. *The effect of pentothal on a mossy fibre response evoked in the cerebellar cortex by a juxtafastigal (JF) electrode.* The diagram illustrates the time course of the P_2 wave depression following the injection of 4 mg/kg of pentothal, the control being 100%. The 3 specimens are the average records of 25 responses taken before (Control) and 8 and 45 min after the pentothal injection

3. The Action of Pentothal on the Mossy Fibre Responses Evoked by Transfolial and Juxtafastigial Electrodes

The lack of a P_2 wave evoked by a nerve volley in the animal under a small dose of pentothal is in contrast with the well known observation that a P_2 wave can be evoked by stimulating the MF afferents close to the cerebellum (TF or JF electrodes) even with a dose of 35 mg/kg of sodium nembutal (Eccles, Sasaki and Strata, 1967; Sasaki and Strata, 1967; Bisti *et al.*, 1971). Therefore, we have investigated whether the P_2 wave evoked in the unanaesthetized decerebrated cat by stimulating directly the MF afferents was affected by the same doses of pentothal which suppress or heavily reduce the P_2 wave evoked by peripheral stimulation. Our experiments show that stimulation by either the TF or the JF electrodes evokes a depth profile in the cerebellar cortex which does not differ qualitatively from that described in the cat under barbiturate anaesthesia (Eccles, Sasaki and Strata, 1967; Sasaki and Strata, 1967). The same depth profile has also been found in the intact unanaesthetized cat (see Fig. 1 in Buchtel *et al.*, 1972). The injection of 4—8 mg/kg of pentothal affects the P_2 wave, but only slightly, and complete suppression has never been found. Figure 4 shows an example where 4 mg/kg of pentothal induced one of the strongest reductions of the P_2 wave evoked by a JF stimulation. It can be seen that following the pentothal injection there is a clear reduction of the P_2 wave, which reaches a value of 70% of the control level after 4—8 min and then gradually recovers in 30 min. A reduction of the P_2 wave following an injection of 15 mg/kg of pentobarbital can be appreciated in Fig. 2 of the paper by Bloedel and Roberts (1969), although these authors did not comment on the effect.

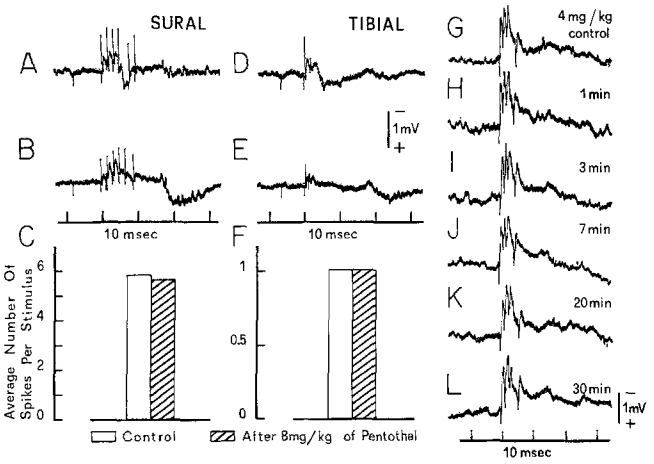

Fig. 5. *The effect of pentothal on the unitary response of mossy fibre afferents evoked by limb nerve stimulation.* In A a single shock to the sural nerve evokes a burst of 6 action potentials, whereas in D the tibial nerve evokes only one action potential. Ten minutes after the intravenous injection of 8 mg/kg of pentothal, the number of evoked spikes is not altered (B and E). The average number of spikes per stimulus evoked before and after the pentothal injection, computed in 30 trials, is reported in C for the sural nerve and in F for the tibial nerve. G—L show the response of another unit to stimulation of the tibial nerve before (Control) and at various interval after the injection of 4 mg/kg of pentothal

4. The Action of Pentothal on Evoked Unitary Activity

Among the several types of units which can be recorded in the cerebellar cortex we have concentrated our attention on 2 types which could be identified with confidence. They are the MF afferents and the Purkinje cells. The former type has been identified according to the criteria of short latency (6.5—10 msec, which is, in any case, earlier than the N_2 wave), and the typical burst discharge as indicated by Eccles *et al.* (1968a) and Eccles *et al.* (1971a). Purkinje cells were identified by the presence of two types of spikes one simple and the other complex (Thach, 1967, see Eccles, Ito and Szentágothai, 1967). We have tested the action of 4—8 mg/kg of pentothal on 12 MF afferents and on 12 Purkinje cells.

A typical behaviour of MF afferents following pentothal injection is illustrated in Fig. 5. In A is shown the response elicited by stimulation of the sural nerve. The response is a burst of 6 spikes with a latency of 7.9 msec and with a modal interspike interval of 1.7 msec. The first spike precedes the N_2 wave, this wave being followed by a P_2 wave. The same unit was activated also by the tibial nerve, although less efficiently, eliciting one spike with a latency of 6.5 msec, as shown in D. B and E are the records corresponding to A and D respectively, but obtained 10 min after the injection of 8 mg/kg of pentothal. Each stimulus delivered to the sural nerve elicited an average of 5.85 spikes in the control condition and 5.65 after injection of pentothal, as shown in the two columns of C. For the tibial nerve the average was 1.05 before and after pentothal (D). Note in records A and B the presence and subsequent disappearance of the P_2 wave and the increase in the later CF field at a latency of 26 msec. This effect was mentioned above. Similar effects have been consistently obtained in all the MF afferents investigated.

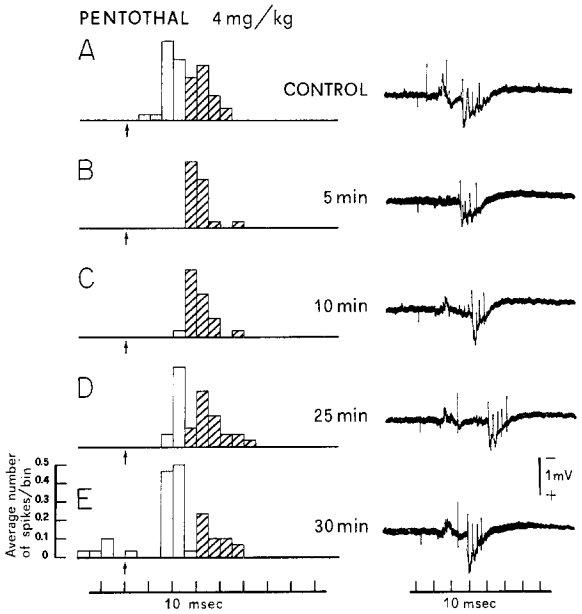

Fig. 6. *The effect of pentothal on the activity evoked in a Purkinje cell by stimulation of a limb nerve.* The sural nerve has been stimulated with an intensity of 3 times the threshold. The histograms at the left represent the average response of 30 trials for the simple spikes (empty columns) and for the complex spikes (hatched columns). At the right are specimen records of unitary responses showing the simple and the complex spikes. A represents the control response. B, C, D, and E illustrate the effect of the intravenous injection of 4 mg/kg of pentothal after 5, 10, 25 and 30 min respectively

The number of spikes in the MF afferents did not show any change also at different time intervals from the injection of pentothal, as shown for a different unit in Fig. 5G—L.

Very different results have been obtained with Purkinje cells. One typical example is displayed in Fig. 6. The specimen at the top is the control taken before the administration of pentothal and shows that following the stimulus artifact signalling the activation of the sural nerve there are two simple spikes and one complex spike. The histogram at the left represents the average of 30 trials and shows that the stimulus evokes MF driven spikes at a latency of 15—25 msec and complex spikes at a latency of between 25 and 45 msec. The peak of the CF response was between 30 and 35 msec. Note that the second simple spike in the top record is preceded by a prominent N_3 wave with a peak latency of 15 msec. Therefore, the MF driven spikes always followed the peak of the N_3 wave. In the other specimens and diagrams below it is shown that following the injection of 4 mg/kg of pentothal there is a complete disappearance of the N_3 wave and of the MF driven spikes and a gradual and full recovery in 30 min. The CF evoked spikes show an earlier peak latency and a reduced variability following pentothal administration. These results on the MF and CF driven spikes have been obtained in all Purkinje cells tested, except one in which the complex spikes were reduced. The effect on the MF driven spikes was always that of a temporary, but complete

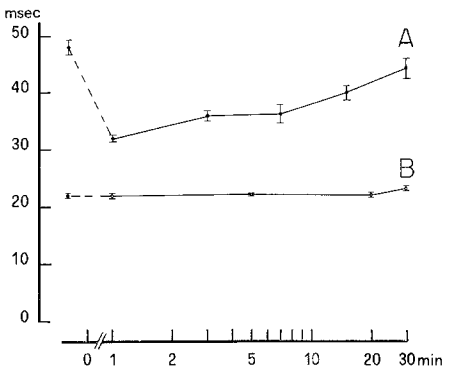

Fig. 7. *The action of pentothal on the latency of the climbing fibre response.* A and B are plots of two units. The average latency with the standard deviation has been computed on 10 responses. At time 0 a dose of 5 mg/kg of pentothal was injected intravenously

suppression. The effect on the CF driven spikes was more clearly seen when the probability of firing was low, and the response showed a longer or more variable latency. Figure 7 shows the action of the same dose of pentothal on the CF response of two Purkinje cells. The unit of A had an average latency around 50 msec. Following the pentothal injection there was a drop in latency to around 30 msec with a decrease also of the standard deviation. The unit in B had a much shorter latency, around 22 msec, and did not show an appreciable change following pentothal administration.

Discussion

Our results show that doses of pentothal as low as 0.5 mg/kg affect the transmission in both MF and CF pathways and that doses of 4—8 mg/kg can suppress completely or almost completely some components of the MF evoked field and the MF driven spikes of the Purkinje cells. In order to explain the mechanism of such an action, we rely on the interpretation of the fields which has already been given (Eccles, Sasaki and Strata, 1967; Eccles, Ito and Szentágothai, 1967; Eccles *et al.*, 1968a; Buchtel *et al.*, 1972). Concerning the effect on the MF system our experiments with limb nerve stimulation have shown first of all that the N_2 wave of the granular layer, as well as the corresponding positive component in the molecular layer, are not appreciably affected by the doses of pentothal used, whereas all the other components are depressed or abolished. Since the N_2 wave is mainly due to the current generated by the excitatory postsynaptic potentials of the granule and Golgi cells, it should be concluded that the administration of pentothal in our experiments affects neither the afferent volley in the MF afferents, nor the synaptic potentials in granule and Golgi cells. It could be objected that with limb nerve stimulation the N_2 wave could also be due to presynaptic activity in MFs, perhaps in a predominant manner. Such a presynaptic component, however, should become negligible in the molecular layer and cannot contribute to the positive wave, which preceedes the N_3 wave. Such a positivity must be due to a passive source provided by parallel fibres and Golgi dendrites to the active sink

(N_2 wave) located in granule and Golgi cells. It is therefore generated only by postsynaptic events. Since this positivity in the molecular layer is not affected by our doses of pentothal (see Fig. 2), we can conclude that the drug does not affect appreciably either the presynaptic activity in the fast MF pathways, or the synaptic potentials in granule and Golgi cells. The conclusion that the activity evoked in this presynaptic fibres is not appreciably affected is also shown by the results obtained by recording directly from the MFs as shown in Fig. 6. Therefore, the suppression of the P_2 and N_3 potentials respectively in granular and molecular layers is interpreted as a block in the axon discharge in granule cells with the consequent suppression of the firing evoked in Purkinje cells. Such an interpretion has already been suggested by Provini *et al.* (1968). The fact that the synaptic potentials in granule cells are not substantially affected by the pentothal, but the axon discharge no longer occurs can be explained by assuming that the drug depresses the excitability of the granule cells at the level of the triggering zone for the action potentials. An alternative possibility is that following the pentothal injection there is an hyperpolarization of the granule cells. The same MF volley impinging upon these hyperpolarized granule cells can evoke a similar or a slightly different excitatory synaptic potential, which, however, no longer reaches the firing level of the cells. Two mechanisms acting separately or in association can be responsible for the hyperpolarization of the granule cells: a direct postsynaptic inhibition exerted by the Golgi cells and/or a disfacilitatory action due to a decreased tonic activity in MF afferents.

It may be surprising that a powerful repetitive discharge in the MF afferents evoked by a limb nerve stimulation is no longer able to fire the granule cells following the small dose of pentothal used here. It might be suggested that with this type of anaesthesia the hyperpolarization is very large and prevents completely the firing of the granule cells. That this is not true is shown by the fact that direct stimulation of the MF afferents can fire the granule cells even with a dose of barbiturate of 35 mg/kg. The effect may be explained by assuming that in the MF-granule cell synapse the transmission is very critical because of its peculiar morphological characteristics.

One granule cell usually has 4 or 5 dendrites. Every dendrite receives only one MF and, therefore, if the cell has 4 dendrites, it will be under the influence of 4 different MFs (Eccles, Ito and Szentágothai, 1967). It is reasonable to assume that direct stimulation of the MF afferents with TF or JF electrodes activates the 4 dendrites of many granule cells, and in these conditions the granule cell fires always at least one action potential, even with a dose of barbiturate of 35 mg/kg. When the stimulus is applied to a limb nerve, the number of dendrites excited synchronously enough to fire an action potential is less than four. We can conclude that those granule cells impinged upon by fast exteroceptive component of the dorsal spino-cerebellar tract have only a few dendrites under the influence of such an input, the other dendrites being under the influence of a slower component of the same tract or of different pathways.

Since barbiturates are assumed to act mainly on the reticular formation (see Rossi and Zanchetti, 1957), it is possible that our small doses of pentothal depress the spino-reticulo-cerebellar pathway. A depression of the reticulo-cerebellar neurones following small doses of pentothal has been already postulated by

Latham and Paul (1971) to explain their effect on the spontaneous activity of cerebellar neurones. Furthermore the intravenous injection of 5 mg/kg of pentothal in an intact free moving animal is sufficient to induce a synchronization in the electrocorticogram (Gordon, Rubia and Strata, unpublished observations). Thus, it is reasonable to suppose that spatial summation is a critical factor in the dendrites of the granule cells. The block of a tonic background on a few dendrites (for instance, those supposedly impinged upon by the reticulo-cerebellar fibres) can be responsible for the block of firing of the granule cells, even if in the remaining dendrites there is a powerful temporal summation. In this sense the granule cell appears as a unit where integration of different MF inputs occurs.

Concerning the CF system, the intravenous injection of pentothal induces an overall facilitation of the transmission in this pathways. This facilitation appears as a large increase of the field evoked by the CF afferents and usually as a shortening of the average latency and increase probability of firing found at a unitary level. The results obtained on the unit activity leave no doubt that the facilitation occurs at precerebellar level, since it is known that the firing of a complex spike by a Purkinje cell is always the consequence of a firing of one or a burst of impulses in the olivo-cerebellar axons.

Løyning *et al.* (1964) have shown that 10 mg/kg of thiamylal sodium injected in a cat under nembutal anaesthesia (30—35 mg/kg), depress the monosynaptic reflex in the spinal cord. The effect is due to a decreased amplitude of the action potentials in the spinal cord terminal afferents and the consequent decrease of the transmitter output and of the excitatory postsynaptic potential in the motoneurone. Therefore, the mechanism of such an action seems different from that occurring at the MF-granule cell synapses. A decrease in amplitude of the single action potentials of the MF afferents was sometimes observed following pentothal injection, but such a reduction was not related to the behaviour of the P_2 wave, and did not show a recovery; therefore, when present, it has been considered as due to a progressive deterioration during the long period of recording.

The results of these experiments on the action of barbiturates on the activity evoked in the cerebellar cortex underline the importance of considering the experimental conditions in which the results have been obtained in order to evaluate the physiological meaning of the projection of the MF and CF pathways to the cerebellar cortex. In experiments aimed at determining the topography of the MF projections, the absence of a P_2 wave does not obscure this projection, if the N_2 wave is well represented. Indeed as pointed out by Provini *et al.* (1968) the size of the N_2 wave is a convenient measure of the MF input. However, the N_2 is sometimes very small and may escape detection if the P_2 wave is absent. In contrast the topography of the CF projection is very restricted in the absence of barbiturate anaesthesia and often not detectable, whereas under this anaesthesia it is large and widespread (Eccles *et al.*, 1968 b). Our results may provide an explanation of the well known sensitivity to barbiturates to the visual projection to the cerebellar cortex, since it has been recently shown that the visual input projects to the cerebellar vermis mainly through the MF input (Buchtel *et al.*, 1972). In the recent results of Maekawa and Sympson (1972) on the visual projection to the vestibular area of the rabbit cerebellum, which occurs only through

the CF system, the absence of MF input may have been due to the barbiturate anaesthesia.

Disagreement on the fine topography of the CF projection from limb nerves obtained by different authors may also be at least in part dependent on the anaesthesia. Oscarsson (see Oscarsson, 1969) has described on decerebrate cats, which however were operated under pentobarbital anaesthesia, a fine projection in sagittal strips of the CF input from limb nerve. Eccles *et al.* (1968b) and Provini *et al.* (1968) working under barbiturate anaesthesia have not found clearly such an organization in strips.

Several other such discrepancies may be found also in the older literature (see Dow and Moruzzi, 1958).

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Dr. P. Strata
Laboratorio di Neurofisiologia del CNR
Via S. Zeno, 51
56100 Pisa (Italy)