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PATTERNS RESPONSES OF PURKINJE CELLS IN CATS TO PASSIVE DISPLACEMENTS OF LIMBS, SQUEEZING AND TOUCHING

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It is interesting to note that the majority of studies on the functions of cerebellum made in recent years was concerned mainly with the intrinsic organization of this organ (cf. Eccles et al. 1967), with its relations to other parts of the brain (cf. Jansen 1959) and with distribution of the pathways reaching the cerebellum from the spinal cord (cf. Oscarsson 1967, Brodal 1967). On the other hand relatively few papers were devoted to the problem of cerebellar representation of peripheral stimuli. This problem was attacked with the macroelectrode technique by Dow and Anderson (1942), Snider and Stowell (1944) and Combs (1954). Adrian (1943) was the first author who applied the microelectrode method. His experiments were performed on anesthesized or decerebrate cats and anesthetized monkeys. Brookhart et al. (1950) used decerebrate cats. In both these series of experiments no attempts were made to identify the units from which the discharges were recorded. Thach (1967) in his first study experimented on anesthetized cats and was mainly concerned with the responses of granule cells to peripheral stimulations. In his second paper (1968) he experimented on unanesthetized monkeys and studied responses of the Purkinje units to rapidly alternating arm movements established as instrumental reflexes.

In this series of papers we are concerned with the detailed analysis of the responses of single Purkinje cells to various kinds of peripheral stimulation. The present paper deals with "natural" stimuli produced by passive displacements of limbs in cat. For the sake of comparison exteroceptive stimuli consisting in squeezing and touching of the limbs were also applied.

In order to eliminate the influence of other parts of the brain on the cerebellum the experiments were performed on decerebrate unanesthetized cats.

MATERIAL AND METHODS

Preparation. Ten cats were used in these experiments. Under short-acting anesthesia (Veritol) both common carotid arteries were freed, the trachea, one saphenus vein and artery were cannulated. Thereafter the animal was fixed in the stereotaxic apparatus, mounted on a heavy stand and the body was supported by clamps on vertebral spines in such a way that the legs were free. Under Nembutal anesthesia administered intraperitoneally (35 mg/kg) the bilateral craniotomy reaching backwards to the edge of bony tentorium was done, the dura was opened on both sides, the falx cerebri divided between ligatures, and the carotid arteries were clamped for 10 to 15 min. Thereafter the brain stem was cut at the precollicular level by means of stereotaxic procedure and the cerebral hemispheres were removed.

After transsection the operation field was almost bloodless, but careful sealing of basal arteries was necessary to prevent later bleeding after the dissipation of anesthesia. Stumps of basal arteries were closed with silver clips or coagulated. The cut face of the brain stem was dressed with sponge, and the carotid arteries were released to improve the blood supply to the cerebellum.

The anterior folia of the cerebellum (Larsell 1953) were widely exposed on the right side by removing the bony tentorium covering them. The operation field was then covered with 1.5% agar-agar in Ringer solution to prevent drying of the exposed brain tissue. The rectal temperature was controlled and was maintained at 38±1°C by application of external heat as necessary. In order to avoid an aftereffect of anesthesia and the postoperative shock, no recording was made until at least six hours after surgery. In some of the experiments during the recording procedure the animals were temporarily immobilized with flaxedil administered intravenously and passive ventilation was instituted.

In nearly all decerebrate preparations the arterial blood pressure was at the level of 110—120 mm Hg, and there was a spontaneous regular respiration. The preparations were so flaccid (particularly during the earlier periods of experiments, when the Nembutal narcosis was not completely dissipated) that the limbs offered no considerable resistance to manipulations.

Recording and stimulation techniques. The recording was made either with tungsten microelectrodes (Hubel 1957) with resistance of 0.5—5 Mohm at a frequency of 5 to 10 kc, or with micropipettes filled with 2M-KCl, their d-c resistance being 8—12 Mohm. The electrode was connected to a probe of a differential cathode follower input. The probe was fixed in a micromanipulator which allowed placement of the microelectrode in such a way that the puncture was at right angle to the surface of each folium. If the penetration occurs very near the edge of the folium, it is possible to move the electrode parallelly to the wall of the folium precisely along the Purkinje layer (Fig. 1).

The output of the cathode follower led to the P-5 Grass preamplifier. The amplified activity was displayed on the Tectronix type 502 oscilloscope and monitored throughout by a loudspeaker. Single frames at variable speed and continuous moving-film (usually at a speed of 25 mm/sec) records were taken by

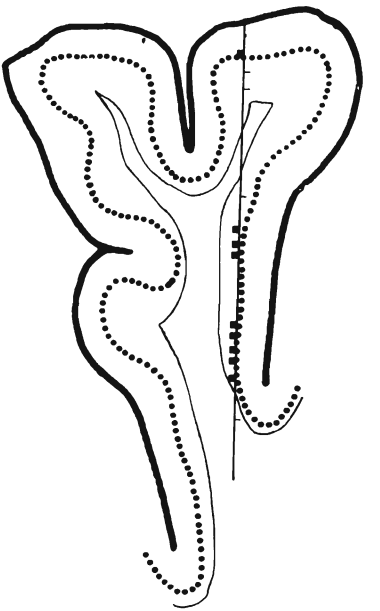

Fig. 1. Example of a track running along the Purkinje layer. Lobulus Va. Dotted line indicates the Purkinje layer. Thin line denotes the border between the granular layer and white matter. Thin dashes perpendicular to the track show sites of recordings outside the Purkinje layer. Squares show records from Purkinje cells

means of Grass Kymograph Camero model C-4. Stimuli were locked on the second sweep and photographed on the same film.

In order to obtain more precise data as to the distribution of frequencies of the observed discharges, the interval histograms of spikes as well as poststimulus histograms were occasionally made (ANOPS–1). Besides this the current frequencies were recorded on the mean-rate frequency meter.

For stimulation passive manipulation of the limbs by experimenter was mainly used. The forelimbs were flexed or extended in finger joints, wrist, elbow and shoulder. The hindlimbs were flexed or extended in hip, knee, ankle and toes' joints. All displacements of limbs had a static character, they lasted usually many seconds or even a few minutes. Sometimes we applied rhythmical displacements, each lasting one to a few seconds.

Besides this, stimulation consisting in strong squeezing (or sometimes pinching) of fingers, toes, paws or tendons was routinely applied. The tactile stimuli at various places on the limbs were applied either when the given part of the leg was grasped by hands in order to change its position, or the skin was stroked in various places.

Before the proper testing of the responses of Purkinje cells along each track, electrical stimulation of the muscles of the ipsilateral forelimb and hindlimb with implanted electrodes was applied and the field potentials from the surface of the cerebellar cortex were recorded. In this way a general orientation of the functional significance of a given region of cerebellum was obtained.

Histological control. Recording sites along the electrode track within the cerebellar layers were identified by small electrolytic lesions placed at the electrode

tip by passing through the electrode a negative current of 5 μa for 5 sec. When the glass microelectrodes filled with 2M KCl were used for recording, they were saturated with dye and the staining was done by passing a negative current of 15 μa for 10 min by a method similar to that of Thomas and Wilson (1965).

After the experiment, the cerebellum was perfused with formaline and the serial frozen sections of 15—20 μ in thickness, stained with Nissl method were made.

RESULTS

In all our ten preparations we made altogether 52 cerebellar penetrations and examined the activity of 301 Purkinje cells. All these cells

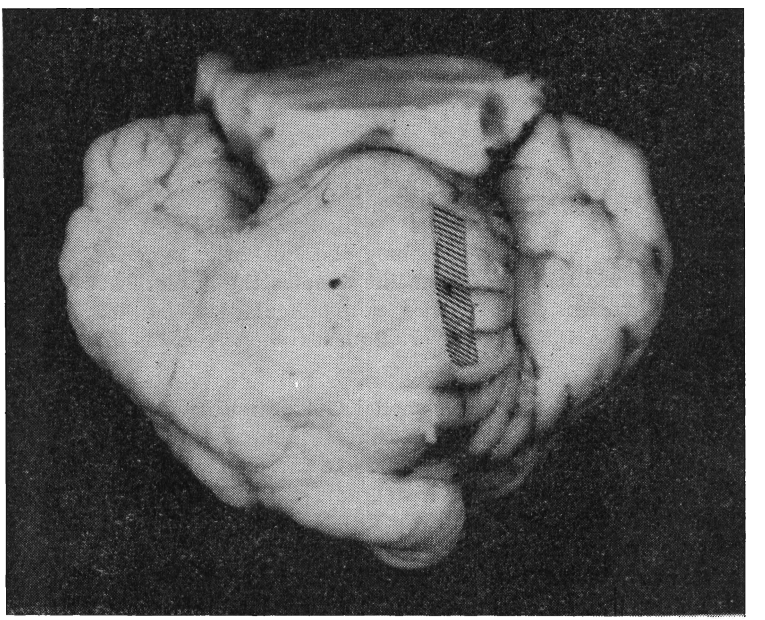

Fig. 2. The area on the anterior lobe of cerebellum from which penetrations were made

were situated in the intermediate zone of the right anterior lobe, lobuli V, IV and III; with deeper penetrations lobulus II was also reached (Fig. 2).

The identification of Purkinje cells was made on the basis of the following evidence: (i) very high and virtually stable amplitude of spikes, as opposed to small and irregular spikes of granule cells; (ii) the existence of inactivation responses (Granit and Phillips 1956), 1957) otherwise called "complex" spikes (Thach 1967) believed to be the effects of impulses delivered by climbing fibers; (iii) the layer of their localization — not less than 350 μ beneath the surface of the cerebellum; (iv) the histological control of their location within the Purkinje layer (Fig. 3).

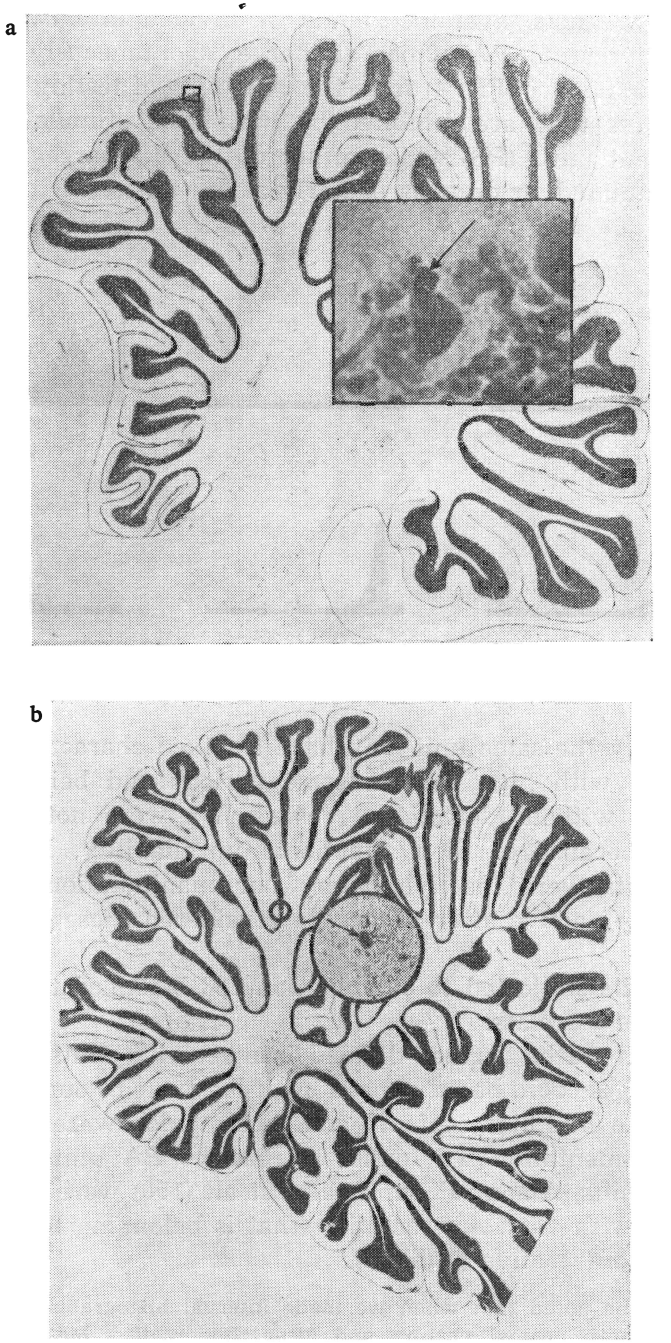

Fig. 3. Histological control of the location of Purkinje cells from which discharges were recorded. a, the Purkinje cell was located in lobulus V; b, the Purkinje cell was located deep in lobulus V. Arrows indicate places of marking

All units we have examined could be divided into two classes: (i) primarily active units (PA) which discharge "spontaneously" at constant rates of 25—80 per sec (Fig. 4) from the beginning of testing and continue to do so unless they are inhibited by peripheral stimulation; and (ii) primarily silent units (PS) which either do not discharge at all, unless properly stimulated, or do so irregularly at low rates.

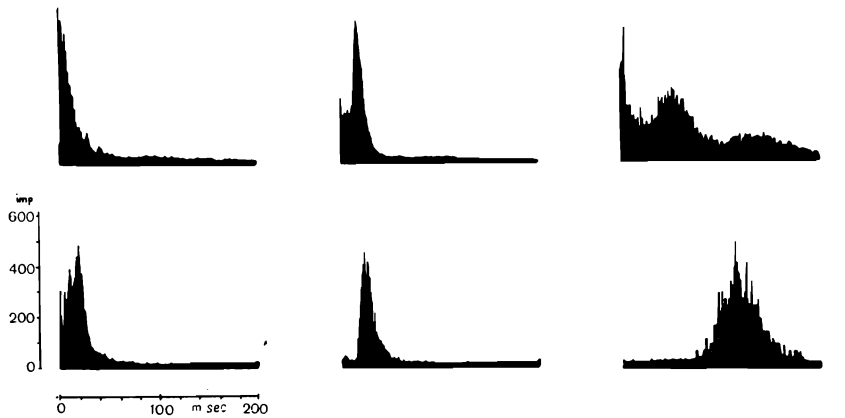

Fig. 4. Interval histograms of "spontaneous" activity of six different Purkinje units

Occasionally the same unit may have a mixed character, discharging spontaneously with high rate at some periods and being inactive at other periods without detectable reasons. We were not interested in those units, because of their functional unreliability. In some other cases the units were inactive before our manipulations but became "spontaneously" active after them. We considered these to be PS units (see below).

Among units subjected to examination 133 belonged to the PA class and 168 to the PS class.

PA units could be further divided into reactive units, that is, those whose discharges could be influenced by at least one of our manipulations (as a rule with inhibitory effect), and those which were non-reactive [1]. In our experimentation we found 91 reactive PA units and 42 non-reactive PA units. Among PS units almost all (159) were reactive: there were 9 units with very slow activity (that is belonging to the PS class) which were non-reactive (Table I).

[1] It should be noted that when we made interval histograms of the PA non-reactive units with normal posture and after flexion of a leg we could detect some small difference in the distribution of the frequencies of discharges which was undetectable by mere observation. We were not concerned in this study with more thorough examination of this phenomenon.

Table I

The numbers and percentages of Purkinje units of various characters examined in this study

Purkinje cells	Non-reactive numbers	%	Reactive numbers	%	Non-reactive and reactive numbers	%
Primarily inactive	9	3	159	53	168	56
Primarily active	42	14	91	30	133	44
Primarily active and inactive	51	17	250	83	301	100

The total number of units (of both PA and PS classes) reactive with regard to any of our manipulations amounted to 250. Of them, 231 units (92.4%) reacted to passive movements of limbs, 87 (34.8%) to squeezing of distal parts of the limbs, and 17 (6.8%) to touching or stroking. (The sum of these three numbers is higher than 250 because as a rule each unit reacted to two or even three modalities of stimuli.)

Below we present separately the functional characteristics of each of these groups of reactive units.

Responses to passive displacements of limbs

The responses of Purkinje units to passive movements were in most cases very regular and uniform. If the unit belonged to the PS class, a proper manipulation produced at once its repeated discharging with the usual rate of about 60 spikes per sec, which continued throughout the period of displacement of the leg, even if it lasted for a number of minutes. This discharging stopped immediately when the leg regained the previous position (Fig. 5). If the limb was repeatedly flexed and extended every few seconds, the unit followed faithfully these manipulations (Fig. 6). In other words the passive displacements of the limbs produced a kind of all or nothing response with no clear gradation.

On the contrary, if the unit belonged to the PA class, it was immediately silenced by an appropriate passive displacement of the limb and returned to its previous activity when the displacement was discontinued (Fig. 7).

Although this was a general picture of the responses of Purkinje units, in some cases we encountered somewhat different responses.

Occasionally we found PA units which reacted to a passive displacement of the leg by still further increase of the rate of discharges, attaining the unusual value of 100 per sec (Fig. 8). In other cases we observed PS units with very rare discharges in which the passive

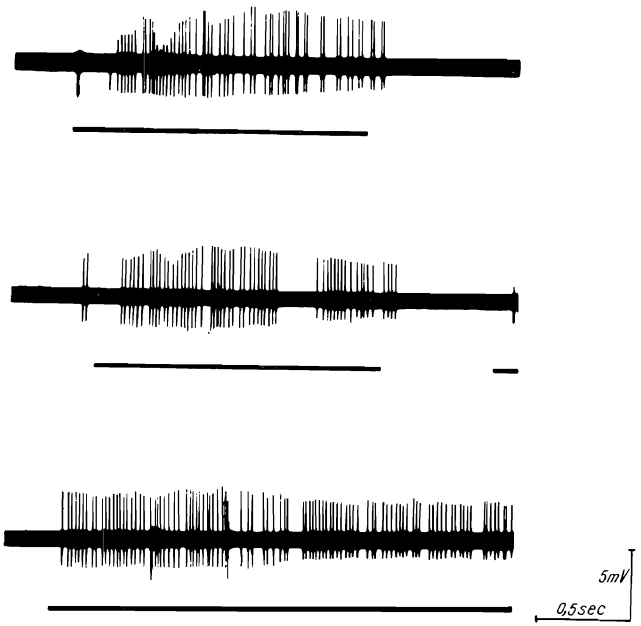

Fig. 5. A PS unit reacting by excitation to the elbow flexion of the ipsilateral foreleg. Horizontal line indicates the duration of flexion

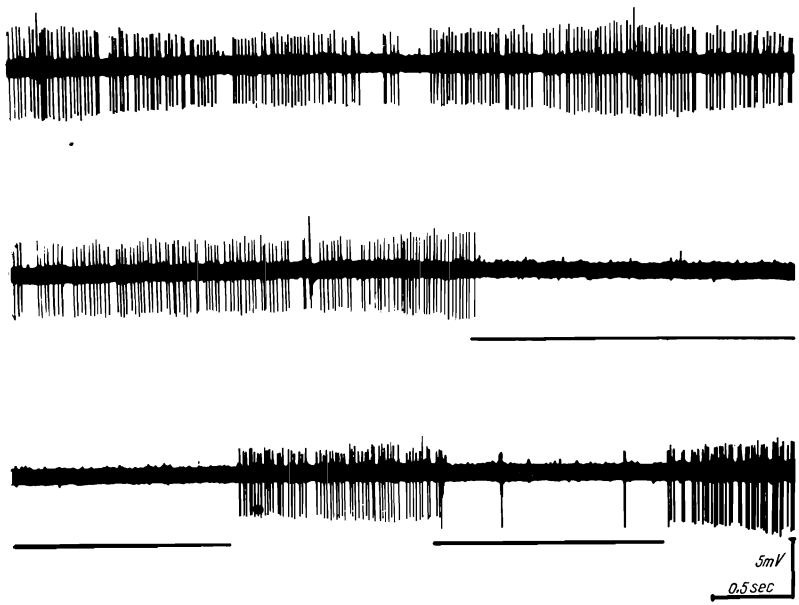

Fig. 6. A PS unit reacting to repeated flexion of ipsilateral knee

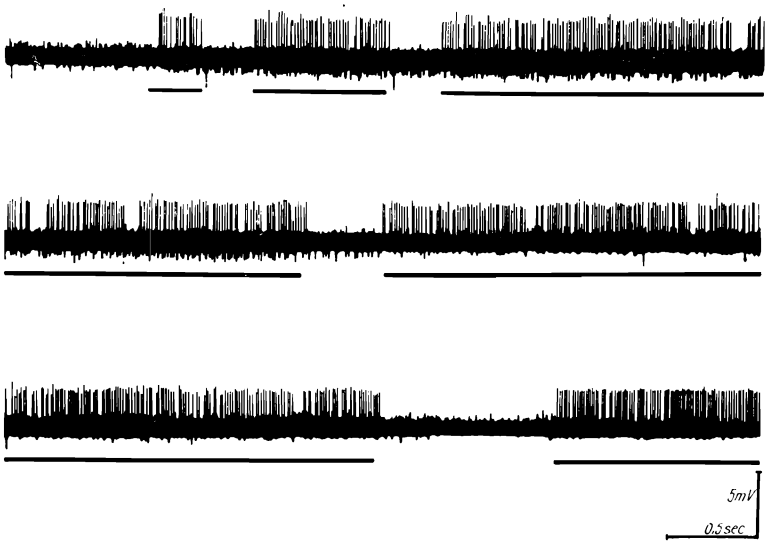

Fig. 7. A PA unit reacting by abolition of discharges to elbow flexion of the ipsilateral foreleg. The line below the record denotes the duration of flexion

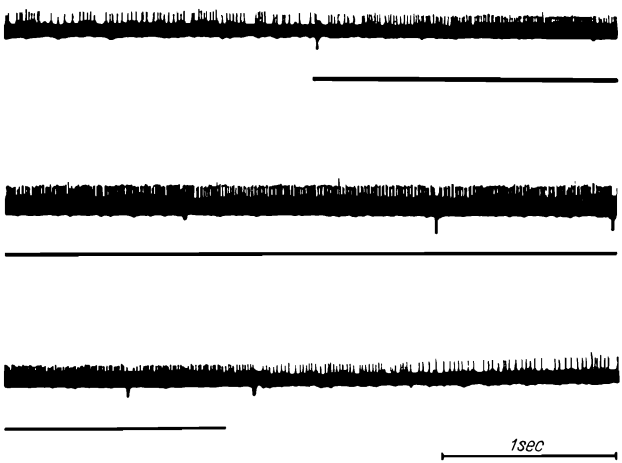

Fig. 8. Acceleration of discharges of a PA unit by flexion of the contralateral knee. Spontaneous activity, 40/sec. Activity during flexion, 100/sec

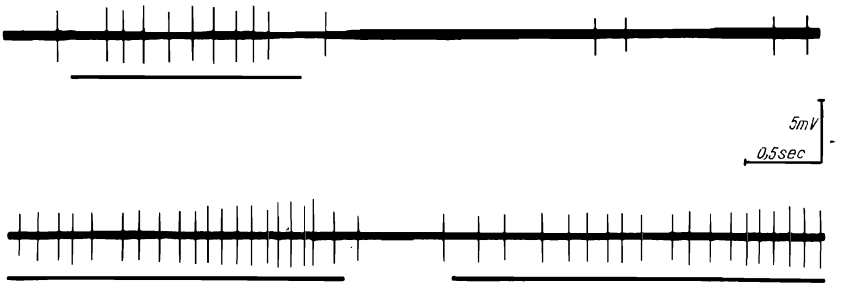

Fig. 9. A PS unit reacting by moderate rate of discharging (about 10/sec) to flexion of ipsilateral hindleg

movement produced an increase of their rate to only about 10 per sec (Fig. 9). Finally, in some cases the PS units, after a number of manipulations, became PA units, that is they started to discharge continuously, although the position of the legs was the same as it was before testing (Fig. 10). It may be seen from the interval histograms that the rate of discharges of these converted units is exactly the same as that during the periods of stimulations.

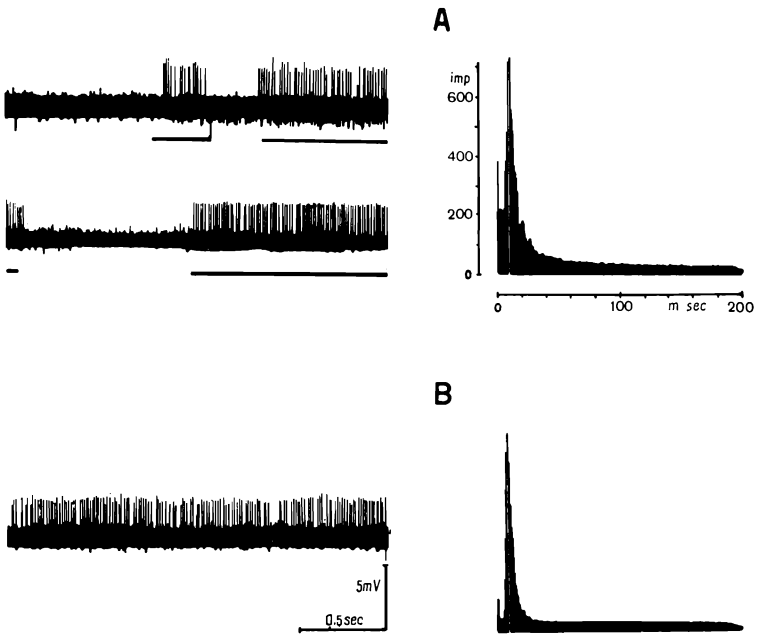

Fig. 10. A PS unit which after a number of responses to knee flexion of the ipsilateral hindleg started to discharge spontaneously. On the right the interval histograms of this unit reacting to steady flexion (A) and spontaneously (B)

The types of passive movements producing the excitatory responses of PS units, or inhibitory responses in PA units, are represented in Table II. For simplifying the presentation of our data, we denoted as the distal portions of the limb fingers and wrist in the foreleg and toes and ankle in the hindleg; we denoted as the proximal portions of the limb, elbow and shoulder in the foreleg, and knee and hip in the hindleg.

It may be seen that the movements of the ipsilateral limbs with respect to cerebellar recording were much more effective than those of contralateral limbs; the only exception was the flexions of the contralateral hindlegs, which were numerous, because the investigated unit reacted usually not only to the flexion of the ipsilateral hindleg, but also to the flexion of the contralateral leg (see below). It is also seen that the responses to flexions of the limbs are far more numerous than those to extensions which were rather exceptional. Therefore, in our further description the term "passive movement" is tantamount to "passive flexion". The excitatory responses of PS units were in general more frequent than the inhibitory responses of PA units, because, as stated before, the former units were more numerous than the latter ones (see Table I).

The further important characteristic of the Purkinje cells is that whereas some of them reacted to the movements of only one joint, others reacted to the movements of several joints of the same limb. Furthermore, a given unit reacted either to the movements within one limb, or to the movements of two limbs or more. Taking into account the number of all possible combinations of limbs and joints the particular units reacted to, it appeared to be simply amazing. Therefore, we were compelled to simplify this whole picture by dividing each limb into the proximal and distal portions and to separate units into those which reacted to the movements of one limb and those which reacted to the movements of more limbs. The various combinations of the limbs the movements of which converge to particular Purkinje units are shown in Table III.

Taking all this diversity into account we may see that the units representing the movements of the forelegs and of the hindlegs differ considerably.

As far as the forelegs are concerned, the units reacting to the proximal portions of the limbs were more numerous than those reacting to the distal portions (cf. Table II). On the other hand, the units reacting to the manipulations of both proximal and distal portions were not very frequent. Furthermore, the units representing the movements of the ipsilateral foreleg only (one-limb units) were much more numerous than

Table II

Various types of passive movements producing responses in Purkinje units

Limb	Part of limb	All units		Units representing flexion of one limb only		Units representing flexion of more limbs		Units representing extension of one limb only		Units representing extension of more limbs	
		excit.	inhib.	excit.	inhib.	excit.	inhib.	excit.	inhib.	excit.	inhib.
Ipsi foreleg	proximal	35	22	28	9	6	10		1	1	2
	distal	28	17	24	15	4	2		1		
	proximal and distal	14	5	5	1	8	4			1	
Contra foreleg	proximal	7	6	2		4	5			1	1
	distal	4	2		1	4	1				
	proximal and distal	6	3			6	3				
Ipsi hindleg	proximal	47	36	12	10	33	25	1		1	1
	distal	14	12	8	8	2	2	4	1		1
	proximal and distal	13	5	1		10	3	1		1	2
Contra hindleg	proximal	35	29	5	3	29	25			1	1
	distal	1	6			1	5				1
	proximal and distal	9	5		1	8	4			1	

Table III

The responses of particular Purkinje units to various combinations of stimuli

EXCITATORY / INHIBITORY			PASSIVE MOVEMENTS				SQUEEZING & TOUCHING			
			FORE LEG		HIND LEG		FORE LEG		HIND LEG	
			IPSI	CONTRA	IPSI	CONTRA	IPSI	CONTRA	IPSI	CONTRA
PASSIVE MOVEMENTS	FORE LEG	IPSI	11 30	12	11	9	30	3	2	1
		CONTRA	7	1 1	6	7	3	4		
	HIND LEG	IPSI	8	3	9 24	36	3		6	1
		CONTRA	7	3	24	4 5	2		4	1
SQUEEZING & TOUCHING	FORE LEG	IPSI	13	4	1	1	4 12	4	3	1
		CONTRA	4	2	1	1	6	2 2	1	
	HIND LEG	IPSI	1	1	10	4	1	1	1 1	1
		CONTRA	1	1	2	2	1	1	2	

The numbers in squares along the diagonal left-up — right-down denote units which react only to one of the items. Above the diagonal excitatory responses are shown, below, inhibitory responses.

those representing in addition other legs (two-limb units). Among the latter, three units represented the ipsilateral foreleg and hindleg and three units proximal portions of the ipsilateral and contralateral forelegs (Table III). To sum up we may conclude that among units reacting to movements of the forelegs prevailed those representing only one portion of one (ipsilateral) foreleg. As stated before, there were many units which reacted to the movement in one joint only (for instance, bending one finger).

Among the units reacting to the movements of the hindlegs those

representing the proximal portions of the limb were thrice as numerous as those representing the distal portions (Table II). The units representing both portions of one leg were not very numerous (as was the case with the foreleg units). On the other hand, in contradistinction to the foreleg units, the hindleg units relatively rarely reacted to the movements of one limb only, and in great majority of instances they reacted to the movements of the proximal portions of both hindlegs (Table II and III). In other words, the units reacting to the movements of the hindlegs were in most cases two-limb units, representing proximal portions of both hindlimbs.

Since such two-limb hindleg units were so numerous, they were subjected to more detailed analysis. The units reacted mainly to a very strong flexion of the hindlimb in the knee and hip (in prone position of the lying animal it is difficult to bend the hip without bending the knee). In roughly half of all cases there were inhibitory responses of PA units and in half the excitatory responses of PS units. The excitatory responses on both sides were of equal intensity. In some cases we bent both hindlegs simultaneously and we failed to see any further increase of the rate of discharges.

Below we give some examples of other, rather unusual characteristics of the units.

In one preparation a number of units situated along one track reacted exclusively to the knee flexion of the contralateral hindleg and to no other manipulations. In a few cases PS units reacted excitatorily to the knee-hip flexion of the ipsilateral leg, but the simultaneous knee-hip flexion of the contralateral leg produced inhibition of the previous response. There were units which reacted excitatorily to flexion of both hindlimbs, but the wrist flexion of the contralateral foreleg inhibited this response. Finally, there were units which reacted to manipulations of all four legs.

To end this description it is worth while to draw attention to one significant fact often observed in our experiments. If we examined Purkinje units of one track, we found as a rule several units in close vicinity which reacted to our stimuli in a similar or even identical way. Here is an extract of two protocols illustrating this fact:

Cat M 32. Electrode in medial part of lobulus V, on the border of lobulus IV.

Unit 12, depth 4702 μ.
Touching and squeezing of both forelegs without effect. Touching and squeezing of both hindlegs without effect. Flexion of the whole right hindleg gives a strong response (80 discharges per sec). It does not depend on the speed of flexion, but only on the amplitude. Fully stimulus-bound. The same with the left hindleg.

Unit 13, depth 4882 μ.
The unit completely silent. Hip-knee flexion of right or left hindleg gives tonic response. Other manipulations without effect.

Unit 14, depth 4932 μ.
Exactly the same response.

Unit 15, depth 5007 μ.
Full flexion of ipsi- and contralateral hindlegs gives exactly the same response.

Unit 16, depth 5097 μ.
(The unit was marked in the end of recording). Identical properties.

Cat M 32. Electrode placed in lateral part of lobulus IV, on the border of lobulus V.

Unit 50a, depth 290 μ.
Silent Purkinje cell, reacting only to flexion of the right elbow.

Unit 50b, depth 410 μ.
The same.

Unit 51, depth 707 μ.
The same.

Unit 52, depth 907 μ.
Purkinje cell activated by flexion of wrist and elbow of both forelegs and squeezing and touch of fingers of the right foreleg.

Responses to squeezing of the limbs

Although the aim of this paper was to examine the responses of Purkinje cells to the passive displacements of the limbs, we also made tests with their squeezing. It was very strong with a tendency to elicit the reflex of withdrawing the limb. The elicitation of the visible reflex was in most instances successful, but this was not the general rule, and certainly we saw a clear response in Purkinje units, although the limb appeared to be immobile.

The character of the responses in the PS units was quite different from that produced by passive movements. Instead of tonic response with a determined frequency of discharges we saw only phasic discharges consisting of a few spikes (Fig. 11). When a PA unit reacted to squeezing its response was as a rule inhibitory and not excitatory.

The numbers of units responding to squeezing are presented in Table IV. It may be seen that squeezing of the forelimbs was much more effective in producing the responses of Purkinje units, than squeezing of the hindlegs. It is further seen that although in some instances (20 in the forelegs and 1 in the hindleg) squeezing (and sometimes touching) was the only effective stimulation, in most cases the given unit reacted also to the passive displacement of the leg. As a rule such bimodal units reacted to squeezing and passive movements applied to the same

leg, and it happened very rarely that the response of the given unit was elicited by flexion of one leg and squeezing of the other one (see Table III).

Here is an illustrative protocol in which a number of units situated at close distances reacted to the squeezing of the ipsilateral foreleg and to no other stimulation.

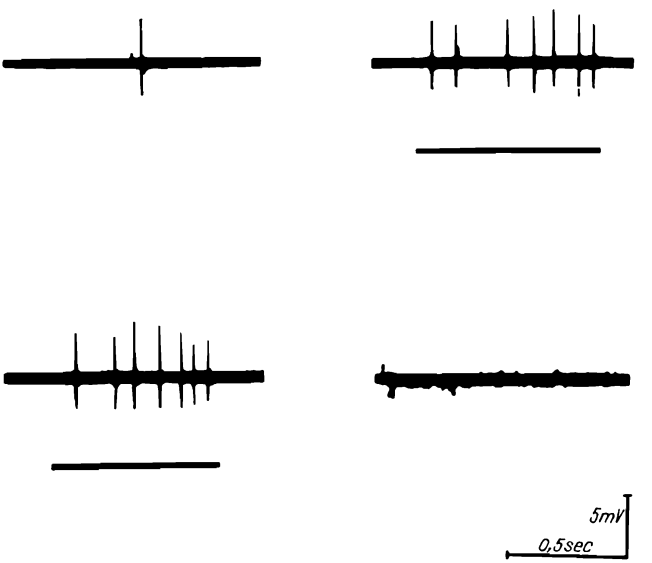

Fig. 11. Response of a Purkinje unit to squeezing of ipsilateral foreleg fingers

Table IV

The responses of Purkinje units to squeezing of the limbs

Limb	All units		Units representing squeezing and touching without passive movements		Units representing squeezing and touching with passive movements	
	excit.	inhib.	excit.	inhib.	excit.	inhib.
Fore-leg ipsi	45	24	13	5	32	19
Fore-leg contra	6	10		2	6	8
Hind-leg ipsi	9	11		1	9	10
Hind-leg contra	2	2			2	2

Cat MS 2. Lobulus V, the border between folium a and b.

Unit 10, depth 5532 μ.
Purkinje cell with very slow spontaneous activity. Reacts exclusively to the very strong squeezing of the distal part of the right foreleg by acceleration of discharges.

Unit 11, depth 5787 μ.
Purkinje cell fails to react to passive movements, but does react to the squeezing of fingers in the right foreleg and squeezing of the wrist by acceleration of discharges. Only phasic reaction, decreasing with repetition of stimulation.

Unit 12, depth 4684 μ.
(The electrode was moved backwards). Purkinje cell, the same response.

Unit 13, depth 4247 μ.
Analogous unit, analogous responses. Only squeezing of fingers effective. From time to time long series of spontaneous discharges. This is the difference from the preceding units.

Unit 14, depth 4972 μ.
Spontaneously active unit. Squeezing of fingers accelerates discharges, flexion of the leg produces inhibition.

Responses to touching

Since with our rather primitive method of producing passive movements, this manipulation always involved preliminary touching of that limb, this sort of stimulation always accompanied the passive movements. It was easy therefore to see that touching was as a rule completely uneffective with regard to activation of Purkinje cells. This is even more conspicuous if we take into account that, according to our own numerous observations, and those of Thach (1967), granule cells are very often activated by light skin stimulation.

This being so, particular attention should be given to a few cases in which the responses of Purkinje cells to light touch were unmistakable. This occurred altogether in 17 units: for 14 units the touch of the ipsilateral foreleg was effective, for two the touch of the contralateral foreleg, and for one the touch of the ipsilateral hindleg.

Here is the protocol of an illustrative case:

Cat MS 3. The medial part of Va on the border of IV.

Unit 13, depth 997 μ.
Reacts (a) to the light touch of the elbow of right foreleg (very beautifully), (b) the touch of hairs on the upper surface of the elbow zone (Fig. 12). All other manipulations in the elbow joint produce increased discharging. The change of the position in the elbow joint produces tonic activity, but manipulation outside this zone gives no effect. Extension of the elbow joint produces a complete abolition of the spontaneous activity.

Unit 14, depth 1310 μ.
Purkinje cell reacting in exactly the same manner. Manipulations in other regions give no effect.

DISCUSSION

The purpose of the present experiments was to analyse the responses of the Purkinje cells to passive displacements of the limbs, and to compare these responses with those produced by exteroceptive stimuli. It was found that when the preparation recovered from the surgery shock and anesthesia (usually six hours after surgery), and the recording electrode moved along the Purkinje layer, the number of Purkinje units reacting to our manipulations with the limbs was simply amazing: by turning the micromanipulator by steps of one or two hundred μs we succeeded in meeting Purkinje cells which either discharged spontaneo-

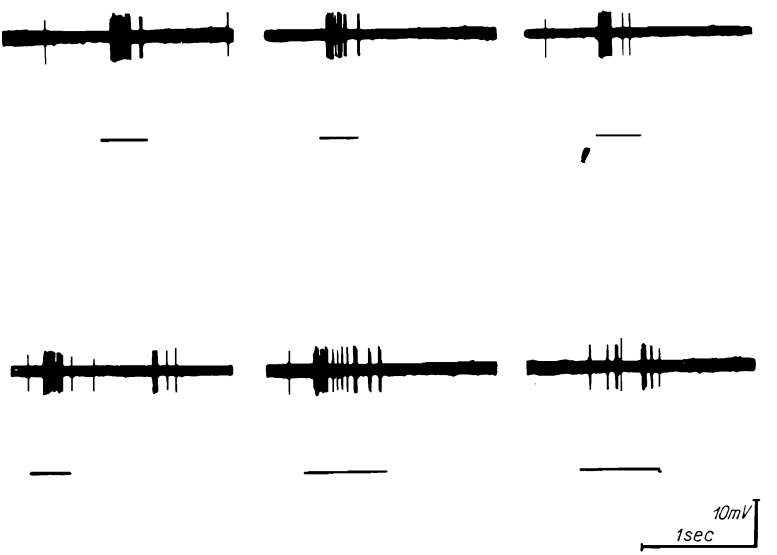

Fig. 12. A Purkinje unit reacting to touch in the elbow zone of ipsilateral foreleg

usly and were inhibited by certain passive movements of a limb, or, on the contrary, were silent and reacted by discharges to these movements. We have the impression that that layer is literally packed with Purkinje cells which can be detected by finding the proper "keys" for their activation.

In most cases the responses to the passive movements, whether they were excitatory or inhibitory, were tonic and strictly stimulus-bound. They arose at a definite position of the given limb and stopped when this position was changed. We failed to discover any clear adaptation of the response even after a period of time lasting several minutes.

This fact seems to throw some light upon the so called spontaneous activity of the Purkinje cells observed by all authors studying the

function of cerebellum. If a unit can be thrown into action for an indefinite period by a given posture of the limb or silenced for an indefinite period by changing the posture, we can conclude that its activity or silence is to a great extent under the control of proprioceptors. In other words, we would assume that the "spontaneous" character of the discharges of Purkinje units would be nothing else but the reaction to a given continuous postural pattern. On the contrary, the full abolition of discharges produced by changing the given posture should be due not so much to inhibition of the units concerned, but to their inactivity produced by the fact that the new posture does not excite the given unit. The problem of what is the share of the cerebral cortex in this dynamics should be elucidated by special experiments.

By accepting this hypothesis we may easily explain the "spontaneous" transition from rhythmic activity to silence and vice versa, so often observed in Purkinje cells. As is well known, the intrafusal muscle fibres are under the permanent influence of the γ fibers, an influence depending on the higher levels of the CNS including cerebellum itself. Owing to the multiple feedback loops the sensibility of spindles can be changed and thus their discharges may be triggered in the absence of any overt movements of the animal. This conjecture is supported by the fact that quite often we could convert a silent unit into an active one by administering a short series of appropriate stimulations (cf. Fig. 7).

In the present experiments the stimulation of proprioceptors was not dynamic but static. Therefore the question may be asked as to whether the changes of muscular stretch are represented by the same Purkinje units as those representing the maintained stretch, or by separate units. According to the existing experimental evidence (cf. Matthews 1964) the primary afferent endings in spindles are rather concerned with the dynamic aspect of the stimulus (i.e. the velocity of stretching), whereas the secondary endings with the static aspect (i.e. the maintained intensity of stretch). Moreover types of afferents are innervated by separate fibers of different diameters. This may suggest that the appropriate central pathways also do not converge, which would suggest that their end stations in the cerebellum would be different.

Some evidence against this suggestion seems to follow from our experimental data which show that squeezing of the distal parts of the leg producing the flexor reflex often (but not always!) activates the same Purkinje unit which is activated by passive flexion. The problem raised will be the subject of our further study.

The next question to be asked is which receptors are responsible for the activation of Purkinje cells (or their inhibition) by passive movements. It is obvious that these manipulations involve stimulation of:

(i) Golgi tendon organs, (ii) spindles, and (iii) articular receptors. Of these the impulses from tendon organs and spindles certainly reach the cerebellar cortex; whether the same or different Purkinje cells are activated by them is difficult to say. As for the articular receptors, we have no clear evidence as to whether they do or do not participate in the responses of Purkinje units. In a few pilot experiments we injected novocain into the appropriate joint and could ascertain that the response of the Purkinje unit to flexion in this was fully preserved. This evidence, however, cannot be regarded as fully conclusive, since it demonstrates only that the joint receptors are not indispensable for the cerebellar response.

The following important problem to be discussed is that of whether somatic exteroceptive stimulation is, or is not, directly represented in Purkinje units. According to our own experiments touching the skin of the animal or even light pressure failed in general to give any responses in Purkinje cells, unless it was combined with the proper passive movement. This was in clear contrast to the relative ease of obtaining responses in the granule cells to those stimuli. However, strong squeezing of the distal parts of the limbs could be effective, but these stimuli often produced flexor reflex of the leg. If the response was not visible, it could have been restricted to the activation of the γ fibers (Grillner et al. 1969).

Our results are in full harmony with those of Thach (1967). According to Figs. 11, 12 and 13 of his paper he obtained a great number of responses of granule cells to tactile stimuli, but Purkinje cells were activated only by pinching or squeezing of the limb.

Since the tactile stimuli reach the granular layer but are not represented as such in the Purkinje units, it may be supposed that they play a facilitatory role with regard to those messages which come from proprioceptors. In fact, in order to have a full information about the static or dynamic states in the motor system the additional messages from skin and joints may be most helpful.

Although the ineffectiveness of the light touch or stroking with

* After this paper was submitted for publication it was clearly shown (Eccles et al. Brain Res. 1969, 14: 222, and Oscarsson, personal communication) that Purkinje cells are not activated by group I afferents, that is by those afferents which convey information both from primary spindle endings and tendon organs. These data would indicate that the static stretching of muscles activating secondary spindle endings is the main source of information conveyed to the Purkinje cells. On the other hand, neither the dynamic stretching of muscles, nor even the stretching of tendon organs is represented in the Purkinje cels. This latter fact is in excellent agreement with our hypothesis concerning the mechanism of cerebellar function presented in the end of this discussion, and elsewhere (Konorski and Tarnecki 1970).

regard to Purkinje cells is certainly well documented, the exceptions from this rule observed in our experiments should not be neglected. Their explanation is not clear. Either there exist rare Purkinje cells which do react directly to touching or stroking the skin, or these stimuli, because of the high reactivity of a given preparation, can produce a γ reflex and thus lead to stimulation of intrafusal muscle fibers (Hunt and Kuffler 1951, Hunt and Perl 1960) or else we had to deal in these cases with some other units, which were mistaken by us for Purkinje cells.

As for the functional characteristics of particular Purkinje units, we found that in spite of their great diversity, which seemingly fails to obey any rules, some general principles concerning the frequency of encountering particular types of units seem to be clear: the units representing ipsilateral limbs are much more numerous than those representing the contralateral limbs, and the units reacting to the extension of the limbs are much less common than those reacting to flexion.

Whereas the first observation is certainly true, the second requires an important correction. In our experiments the cat was lying in a prone position with the limbs moderately extended. We found, indeed, that farther extension of the limbs failed to produce any reaction of the Purkinje units, but we must keep in mind the fact that almost half of our units which reacted by inhibition to the flexion of a definite leg, returned to their "spontaneous" activity when the leg was again extended. Therefore it seems reasonable to regard all such units as those which react precisely to the given limb being in an extended position. If so, we may conclude that there are almost as many units reacting to extension as those reacting to flexion.

The following important fact discovered in our study was that whereas some Purkinje units were "monoarticular", that is they reacted to the displacement of a limb in only one joint, the other ones were "polyarticular" — they reacted to several passive movements within one limb, or to movements of several limbs. It is significant that whereas the units representing the foreleg are in most cases monoarticular, those representing the hindleg are mostly polyarticular. This rule certainly reflects the well known behavioral fact that isolated movements and postures within one joint are necessary for the skilled actions of the forelegs, whereas the movements of the hindlegs are much less emancipated owing to the complex postural coordinations.

The most conspicuous and frequent type of polyarticular units is when a unit reacts to passive hip-knee flexion of either the ipsilateral or the contralateral hindleg. The characteristic feature of these units is that they usually react to full flexion of the limb, that their responses

are strictly stimulus-bound, and that flexion of both limbs elicits the discharge of roughly the same rate as that of one leg.

In his recent monograph Konorski (1967) drew attention to the fact that if the cerebellar cortex is regarded as a "receptive surface" for kinesthetic stimulations, then the pathways linking this surface with the precentral ("motor") area of the cortex are strikingly similar to those linking the cutaneous and joint receptive surface with the post-central ("somatosensory") area (Fig. 13). From this fact Konorski drew a conclusion that the functional role of the cerebellar cortex may consist in transformation of the messages concerning stretching of tendons and muscles detected by Golgi organs and spindles respectively into the messages informing about movements.

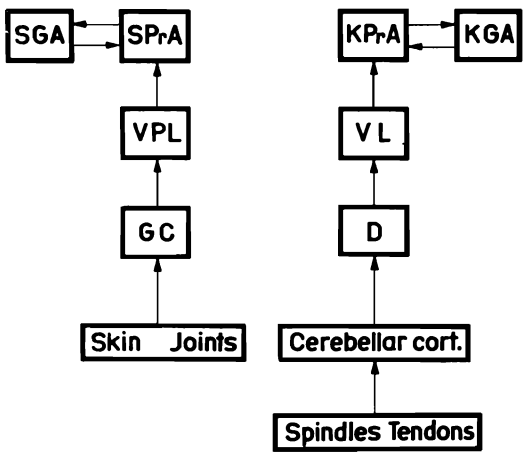

Fig. 13. Block models of somesthetic and kinesthetic afferent systems (simplified) Left, somesthetic afferent system: GC, nuclei gracilis and cuneatus; VPL, ventral postero-lateral thalamic nucleus; SPrA, somesthetic projective area; SGA, somesthetic gnostic area. Right, kinesthetic afferent system: D, dentate cerebellar nucleus; VL, nucleus ventralis lateralis thalami; KPrA, kinesthetic projective area; KGA, kinesthetic gnostic area (nucleus ruber is omitted for the sake of simplicity). Note, the clear symmetry between the two systems except for the peripheral segment of the kinesthetic afferent system

The results described here seem to throw some light upon the problem of how the cerebellum fulfills this transformation.

As was shown in recent years (cf. Eccles et al. 1967) Purkinje cells exert an inhibitory effect upon the neurons of intracerebellar nuclei being the relay station between the cerebellum and the cerebrum. Since passive movements produce excitation of Purkinje cells, this means that the messages about these movements inhibit this relay station.

It is known that the spinocerebellar tracts convey impulses not only to

the cerebellar cortex but also directly to the intracerebellar nuclei delivering there excitatory impulses (Eccles et al. 1967).

Let us assume that impulses originating in spindles impinge only an Purkinje cells, whereas those originating in tendon organs reach directly intercerebellar nuclei. As the result of this arrangement the purely passive stretching of muscles, involving activation of both tendon organs and spindles, fails to excite the intracerebellar nuclei because of the inhibitory effect of Purkinje cells. On the contrary, the active movements executed against resistance activate the tendon organs but they silence the muscle spindles because of the shortening of the muscle (cf. Matthews 1964); in consequence, these movements produce activation of the neurons of intracerebellar nuclei which activation is transferred into the cerebral cortex. In this way the cerebellum serves for blocking the messages about passive movements in their way to the brain and transferring only those messages which concern active movements against resistance. The more detailed development of this concept is presented elsewhere (Konorski and Tarnecki 1970, in press). The experimental work verifying this hypothesis is now in progress.

SUMMARY

1. The responses of the Purkinje cells to passive displacements of the legs were studied in decerebrate unanesthetized cats.

2. The responses of primarily inactive or slowly discharging Purkinje cells to those manipulations consist in discharges continuing with constant rate throughout the period of preserving a given posture. The responses of primarily fast active Purkinje cells consist in complete abolition of their discharges.

3. A given unit may react to the particular displacement in one joint only, or to displacements in more joints in a given limb, or else to displacements of more than one limb. The units reacting to manipulations of the ipsilateral forelimb are mostly monoarticular, those reacting to manipulations of the ipsilateral hindlimb are mostly polyarticular.

4. The displacements of ipsilateral limbs, particularly the foreleg, are more effective in eliciting the responses of the Purkinje units, than are the displacements of the contralateral legs.

5. Polyarticular units may react to the displacements of very diverse combinations of joints. The most frequent combination is the flexion of the proximal portions of ipsilateral and contralateral hindlimbs.

6. Strong squeezing of the distal portions of the legs, usually evoking the flexor reflex, may elicit the response of Purkinje cells. The light touching of the limbs or their stroking only exceptionally produces

responses in Purkinje cells. It is hypothesized that squeezing and touching can produce these responses only when they reflexly activate spindles through the γ fibers.

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