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THALAMOGENIC MOVEMENTS IN CATS: THEIR CHARACTERISTICS AND DEPENDENCE ON THE CEREBRAL CORTEX

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Numerous studies concerning the effects of electrical stimulation of the cerebral cortex, performed either in waking animals by means of implanted electrodes, or in waking patients during neurosurgical operations, have shown that not only the motor area, but also a number of other areas are electrically "excitable"; that is, their stimulation gives rise to various motor activities (Foerster 1936, Penfield and Boldrey 1937, Dusser de Barenne et al. 1941, and others). In particular, stimulation of the sensory area in waking cats was shown to produce isolated movements of the contralateral limb (hindlimb or forelimb), similar to, but not identical with, those arising from stimulation of the motor area (Tarnecki 1962a, Tarnecki and Konorski 1963). The chief differences are: longer latencies, gradual and not abrupt initiation and termination, higher thresholds, and a more natural character. The fact that, with respect to the hindleg, only those movements produced by stimulation of the sensory area, but not of the motor area, are instrumentally conditionable (Tarnecki 1962a, Tarnecki and Konorski 1963) proves that the former movements have a "reflex" origin (cf. also Konorski 1967).

To our knowledge there were no systematic studies on the effects of stimulation of the ventrolateral (VL) and ventral posterolateral (VPL) thalamic nuclei, that is, those nuclei which have direct connections with the motor and sensory cortex respectively. Therefore, the purpose of the present study was to fill this gap.

MATERIAL AND METHODS

The experiments were performed on twelve cats in an experimental box of the size 85×50×75 cm. In the front side of the box there was a moving glass wall through which the experimenter observed the animal.

In each cat in two operations separated by an interval of a few days bipolar stainless steel electrodes of a diameter of 0.2 mm and 0.5 mm tip separation were implanted into the VL and VPL nuclei respectively using a stereotaxic apparatus. The VPL implantation was performed on one side under 35 mg/kg nembutal anesthesia, the VL implantation was performed on the other side under 50 mg/kg chloralose anesthesia. The localization of the electrodes was determined by stimulation with the needle electrodes of the contralateral forepaw and hindpaw and recording evoked potentials from the corresponding nuclei of the thalamus. The thalamic electrodes were fixed in the position of the maximal amplitude of evoked potentials. It should be noted at once that it was much easier to find points responding to stimulation of the forepaw than of the hindpaw.

Two weeks after the final operation the animals were brought into the experimental box (to which they had been habituated beforehand) and the electrodes were connected with a socket connected with the Grass stimulator through a loose soft wire hanging from the ceiling of the box. Thus free locomotion of the animal inside the box was insured.

In a few animals stimulation of various parameters was used in order to choose those which were most adequate for eliciting the isolated movements of either the forelimb or the hindlimb. The current was measured from the voltage drop on ten ohms resistance connected in series with the electrodes. When this was achieved eight animals were trained in instrumental conditioning by reinforcing the thalamogenic movement with presentation of food. This part of the experiment will be described in a subsequent paper (Tarnecki and Konorski 1969).

When the CR training was completed, or, in those animals which were not trained, the stimulation testing was terminated, ten animals out of twelve were subjected to a cortical operation under nembutal anesthesia. In this operation the unilateral sensorimotor area of the cortex, and in some animals in addition the premotor cortex, was removed. The side of the lesion was contralateral to that limb which was used in instrumental conditioning.

Two weeks after this operation the animals were tested in respect to their instrumental CRs (to be described in the next paper) as well as the effects of thalamic stimulation. Testing of stimulation was performed in a part of the box remote from the food well in order to be certain that no instrumental responding was admixed to the evoked movement. In some test experiments the animals were satiated before the session, a measure completely abolishing instrumental responding on that day.

After stimulation experiments and conditioning experiments were terminated, neural tissue surrounding the points of the electrodes was coagulated, the animals were sacrificed and their brains perfused with 10% formalin. The reconstruction of cortical lesions was made and the location of the electrodes was verified using the Klüver staining technique.

RESULTS

Parameters of stimulation. In a pilot study the optimal frequencies of stimulation were established. Beneath we present an example of this exploration. The pulse duration was 1 msec.

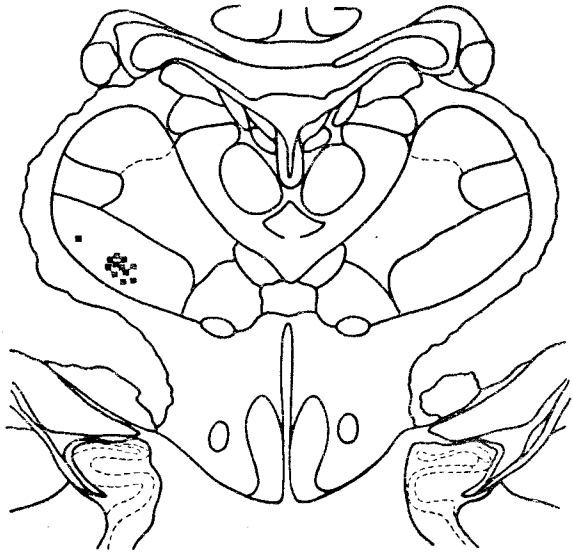
Cat no. 1. Electrodes in the left VPL nucleus. Each stimulation was repeated several times with intervals of a few minutes.

Stimulation	Behavior
1.0 v 50 c/sec	No response
3.0 v 50 c/sec	No response
5.0 v 50 c/sec	Inspects his right foreleg, licks it, remains quiet.
8.0 v 50 c/sec	Disquiet, inspects the leg, then tries to escape.
3.0 v 150 c/sec	Lies down, rubs the contralateral side of the body against the wall, looks at the forepaw and licks it.
5.0 v 150 c/sec	Irregular isolated movements of the foreleg, rubs his body against the wall, after stimulation licks the leg.
3.0 v 300 c/sec	After a latency of about 4 sec isolated and prompt flexion of the right foreleg with a slight turn of the head to the right; sometimes licks his paw. The responses are rapid and regular.

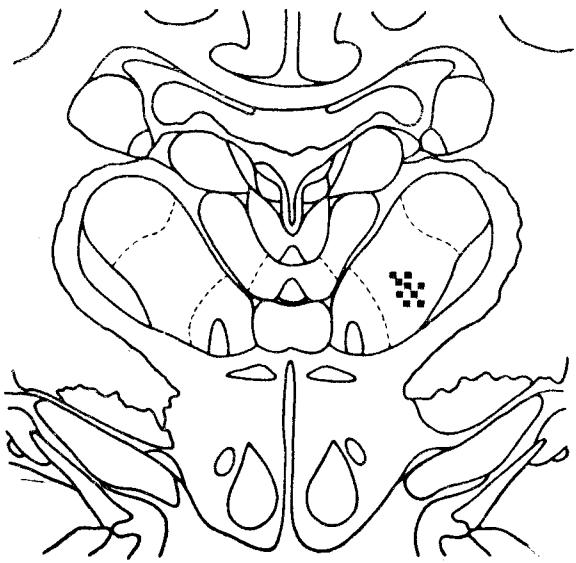
As seen from this protocol, the optimal frequency of stimulation was in this cat 300 c/sec. Since the similar picture was seen in other cats, this frequency was adopted in this series of experiments.

Stimulation of the VPL nucleus. The characteristics of the responses of the animals are given below. The frequency of stimulation was always 300 c/sec, the pulse duration 1 msec. The optimal current of stimulation was 0.2—0,4 ma. The locations of electrodes are presented in Fig. 1a.

Cat no. 1.	3 v.	Isolated and regular lifting of the contralateral foreleg, slight turn of the head towards the leg, licking the paw.
Cat no. 2.	4.5 v.	Rapid high lifting of the contralateral foreleg with the turn of the head in its direction. When during the stimulation food is presented the movement is discontinued and the animal runs normally towards the food well.
Cat no. 3.	1.5 v.	The cat gets up, inspects his body, sniffs.
	3.0 v.	Isolated and regular lifting of the contralateral foreleg.
Cat no. 4.	3.0 v.	Sniffs, lies down.
	5.0 v.	Lifting of the contralateral foreleg, sometimes with turning of the head. Irregular latencies.
Cat no. 5.	4.5 v.	Isolated lifting of the contralateral foreleg, sometimes looks at it. Low amplitudes of the movements.
	6.0 v.	The cat becomes immobile, then tries to escape.
Cat no. 6.	3.0 v.	Rapid and regular lifting of the contralateral foreleg. Continuation of stimulation produces movements of head and neck.



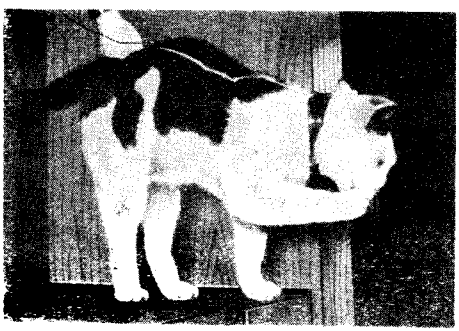
a



b

The placement of the electrodes in the VPL nucleus (a) and in the VL nucleus (b)

Cat no. 7.	5.0 v.	Isolated flexion of the contralateral hindleg obtained when the cat is standing. After stimulation he inspects the leg.
Cat no. 8.	3.5 v.	Small movements of the contralateral foreleg, inspects the leg and sniffs it. Sniffs the floor round the leg.
	4.8 v.	Isolated and rapid movements of the leg. After stimulation inspects it for a long time.
Cat no. 9.	1.3 v.	Lies down and licks various parts of the body.
	3.5 v.	Isolated and rapid movement of the contralateral foreleg. Licks the leg or shakes it as if it were wet (Fig. 2a). If during stimulation the food is presented the animal puts his leg on the floor and runs to the food well.
Cat no. 10.	3.5 v.	Isolated lifting of the contralateral foreleg, sometimes turning the head towards it. After stimulation inspects the floor and sniffs it.
Cat no. 11.	3.5 v.	The cat lies down and rubs his body against the floor, licks his contralateral foreleg or shoulder.
	7.2 v.	High, rapid and repeated lifting of the foreleg, after stimulation long and intense licking of the paw.
Cat no. 12.	7.0 v.	High lifting of the leg with shaking movement (wet leg symptom). After stimulation holds the leg high as if he were afraid to put it down. Sniffs the leg and the floor. After several stimulations tries to escape.



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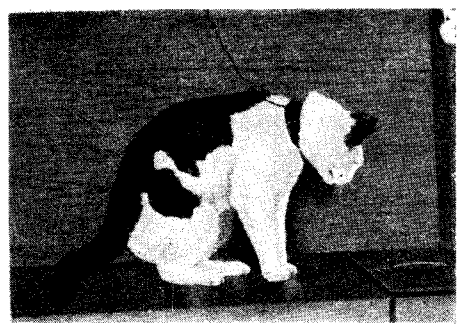


b

Fig. 2. The effect of VPL stimulation in cat no. 9, before (a) and after (b) removal of the sensorimotor cortex. Strength of stimulation 3.5 v

We have presented above the most salient fragments of the protocols which throw light on the character of the movements elicited by electric stimulation of the VPL nucleus with 300 c/sec.

The most frequently observed response consisted in lifting the contralateral foreleg with occasional turning of the head towards it. Only in one animal was the movement of the hindleg elicited. The movements were rapid with veriable amplitudes and latencies amounting to a few seconds. The size and character of the movement often depended on the posture

taken by the animal before stimulation. The responses were regular, if the intervals between stimulations were long (several minutes).

When stimulation was subthreshold with respect to the elicited movement, indefinite, sometimes bizarre, types of behavior were seen: the animal lay down on his back, rubbed his body against the floor or the wall, sniffed around and so on. The effective stimulation was also usually accompanied by additional responses like inspecting the leg involved in the movement, licking or sniffing it, shaking movements, sniffing the place on which the cat stayed. These responses appeared both during stimulation and particularly after its termination.

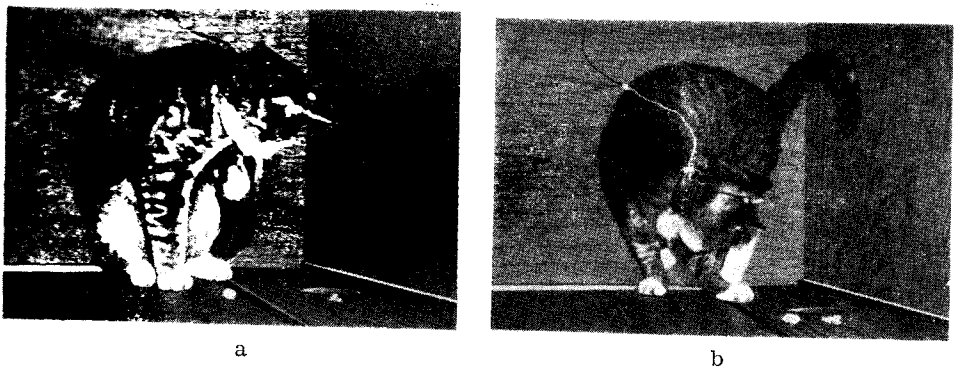
In most cases stimulation of the VPL nucleus did not elicit any aversive symptoms. The animals were not afraid of the exsperimental cage and willingly ate food presented after and even during stimulation. However, if the voltage of stimulation was high (about 7 v) the animals clearly manifested a defensive attitude which consisted in trying to get out of the cage and/or refusing to take food. No epileptic seizures were seen. Finally, it should be mentioned that the motor response elicited by VPL stimulation could be easily inhibited by other activities of the cat. In connection with the instrumental training of the elicited movements, we had many occasions to notice that when the animal heard the click of the bowl placed in the aperture of the food well, he ran towards it on four legs and could use the leg involved for taking food out of the bowl.

Stimulation of the VL nucleus. The optimal current of stimulation was 0.4—0.8 ma. The locations of electrodes are presented in Fig. 1b.

Here are the fragments of the protocols recorded for particular cats:

Cat no. 3.	6.0 v.	Isolated movement of the contralateral foreleg. Long and irregular latency. If stimulation is protracted the movement of the hindleg also appears.
Cat no. 5.	5.0 v.	Isolated and very regular lifting of the contralateral leg with supination of the paw. Supination means that the foreleg turns along its long axis so that the palm is directed inwards. Long latency, the amplitude of the movement gradually rises. The movement is not inhibited by the act of eating.
Cat no. 6.?		Lifting of contralateral forelimb and hindlimb. Isolated movements cannot be obtained.
Cat no. 7.	8.0 v.	Lifting of the contralateral foreleg and stiffening of the neck.
	10.0 v.	Lifting of the foreleg with strong supination. Turning of the head producing a loss of balance, so that the cat falls down on his side and cannot rise till the end of stimulation. No signs of aversion towards stimulation.

Cat no. 8.	6.0 v.	Gradually increasing isolated movement of the contralateral foreleg. Protracted stimulation leads to a strong supination (Fig. 3a). Latency 7—10 sec.
Cat no. 9.	6.5 v.	Isolated movement of the contralateral foreleg with long latency and gradually increasing amplitude; slight supination of the paw. When food is presented the cat tries to approach the food well with the foreleg lifted.
Cat no. 10.	4.0 v.	Clear muscle contractions of the distal part of the contralateral foreleg with clawing. Latency of about 10 sec.
	7.0 v.	Isolated lifting of the foreleg with supination. Latency about 10 sec and the performance of the movement extremely slow. If the animal received food during stimulation he ate it with the foreleg lifted. If stimulation was given at the moment when the animal took food with that foreleg he stopped doing so, or lifted the leg holding a piece of meat, but not putting it into the mouth.
Cat no. 11.	8.0 v.	Isolated lifting of the contralateral foreleg, occasional co-movements of the shoulder and ear. Protraction of stimulation elictis in addition small movements of the hindleg.
Cat no. 12.	8.0 v.	Isolated lifting of the contralateral foreleg with slow forward extension and supination. Latency till 15 sec.



a b

Fig. 3. The effect of VL stimulation in cat no. 8 before (a) and after (b) removal of the sensorimotor and premotor cortex. Strength of stimulation in a 6 v, in b 10 v

As seen from these protocols the character of the elicited movements is quite different from those producted by VPL stimulation. The latency is longer, the increase of the amplitude much slower, the effective strength of current nearly twice as large as in VPL stimulation. The movement has a stereotyped character, the lifting of the leg being accompanied by supination and sometimes extending the leg forward. If the intervals between stimulations are long (3—5 min), the responses are very regular. If stimulation is protracted, or its strength increased, the

movements become generalized: there appears the lifting of the hindleg, movements of the mouth, ear and shoulder, as well as turning the head. The isolated movement of the hindleg was never obtained in these experiments. There were no accompanying symptoms of "paying attention" to the limb, so characteristic for VPL stimulation. Rather there was impression that the animal did not "notice" the movement performed.

The movement was not inhibited by the antagonistic activities (e.g. locomotion or food intake) as was the case with VPL stimulation. Stimulation never had an aversive character and no epileptic seizures were observed. The subthreshold stimulation with regard to the movement of the foreleg did not produce any observable effects.

The effects of cortical lesions on the VPL-produced movements. In five animals (no. 2, 4, 6, 7, 9) the sensorimotor area of the cortex was removed on the same side on which the VPL electrode was implanted. The reconstructions of lesions are presented in Fig. 4. After the ablation, stimulation of the VPL nucleus was retested.

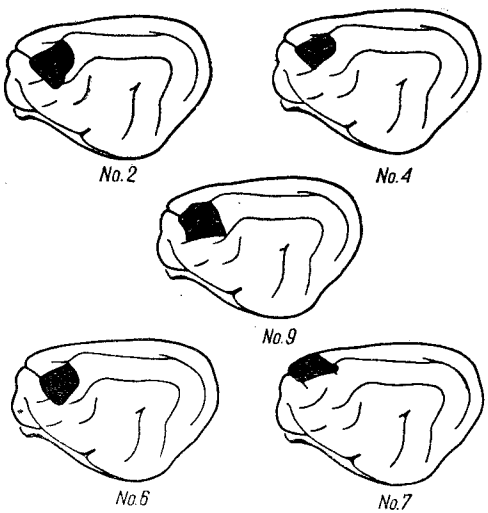


Fig. 4. Cortical lesions ipsilateral to the electrodes implanted in the VPL nucleus. Note that in cats no. 2, 4, 6 and 9 the sensorimotor cortex for the forelimb was removed, whereas in cat no. 7 the sensorimotor area for the hindlimb was removed

The results of these experiments were quite uniform. In all animals the movements observed before surgery were completely abolished (Fig. 2b). When the voltage was increased till 10 or 12 v clear and unmistakable defensive responses were observed accompanied by strong fear. Beneath we give the protocols of some sessions.

Cat no. 4. Removal of the left sensorimotor cortex limited to the foreleg area.

Before operation a regular isolated movement of the right foreleg was elicited by VPL stimulation with 5.0 v, 300 c/sec. The same sti-

mulation after operation produces no response. When stimulation is protracted till 30 sec the animal becomes disquiet, walks around the cage, sniffs and looks round.

8.5 v. After 2—4 sec the cat looks at his foreleg, licks it, then flattens his ears, moves backward and becomes disquiet. After several stimulations he tries to flee from the cage, and becomes aggressive. When touched or stroked, he mews, tries to escape and after more trials attempts to bite the hand of the experimenter. Refuses to take food.

10.5 v. Runs round the cage, sometimes stops abruptly, sniffs, mews, flattens the ears, tries to grasp by teeth the skin on the shoulder. After stimulation sits down in the corner of the cage, licks his claws, paw and the whole right side of the body. Avoids being touched. After prolonged stimulation jumps out of the cage.

12.0 v. Moves hindleg clumsily, then freezes, crouches, pants, looks fearfully around. The movements of the experimenter produce flight reaction.

Exactly the same picture was observed in other cats.

The effects of cortical lesions upon the VL-produced movements. In cats no. 5, 8, 10, 11 and 12 cortical lesions were sustained on the side of the VL electrodes (Fig. 5) and the results of those lesions are as follows.

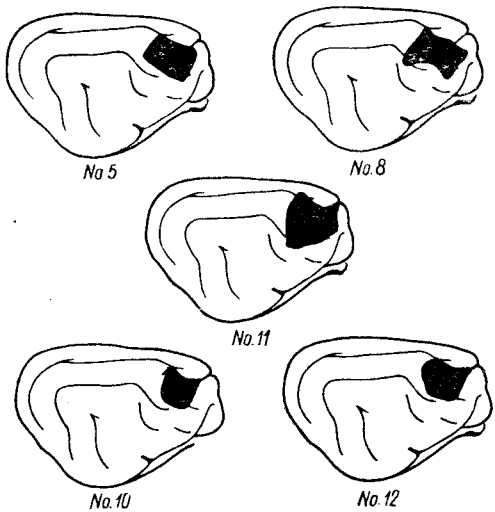


Fig. 5. Cortical lesions ipsilateral to the electrodes implanted in the VL nucleus. Note that in cats no. 10 and 12 the sensorimotor area was removed, whereas in cats no. 5, 8 and 11 the lesion involves also the premotor cortex

Cat no. 10. Ablation of the sensorimotor cortex for the foreleg. Stimulation of the VL nucleus produces the same motor response as before operation. The latency is somewhat prolonged.

Cat no. 12. Ablation of the sensorimotor cortex for the foreleg. The character of the movement produced by VL stimulation is similar to

that before operation, but its amplitude is reduced, and the supination clearly manifested before operation is absent. The response occurs less regularly and sometimes is absent. Increase of stimulation from 8.0 v to 9.2 v makes the occurrence of the movements more regular, but then the turn of the head and the tension of the muscles of the neck is observed. The amplitude of the movement remains low. If during stimulation food is presented the cat takes it willingly.

Cat no. 5. Ablation of the sensorimotor and premotor cortex. The lesion is shallow (in the cruciate sulcus) but extensive.

5.0 v (as before operation). No visible response.

7.0 v. No visible response.

10.0 v. The motor response is similar to that before operation, but its amplitude is lower and supination is absent. Its occurrence is irregular. If stimulation is prolonged till 30 sec, the tension of the neck and clenching of the jaws is seen which continues for 1—3 min after stimulation. After prolonged stimulation the cat is apathetic, is not interested in food, but remains calm. Rhythmic jerking of the head is also observed.

Cat no 8. Ablation of the sensorimotor and premotor cortex.

6.0 v (as before operation). No visible response.

8.0 v. No isolated movement of the leg, strong cramps of the neck, clenching the jaws, difficulties in respiration. Rhythmic jerking of the head. Afterwards the cat is apathetic and does not take food.

10.0 v. Tonic rigidity of the neck, clenching of the jaws, unnatural and tense turning of the head (Fig. 3b), followed by slow lifting of the hindleg and its stretching forward with spreading out the claws. Frequently this movement is stopped by increased turning of the head and body which leads to a loss of balance and the cat's falling down with tense muscles. After the stimulation is withdrawn it lies motionless and after 2—3 min strong and repeated jerking of the head is observed ending with jerking of the whole body. The seizures are followed by general relaxation of the body and immobility.

Cat no. 11. Ablation of the sensorimotor and premotor cortex.

Complete abolition of the isolated movements. Stimulation with 15 v produces general seizures similar to those described in cat no. 8.

Summarizing the effects of the VL stimulation after cortical lesions we can conclude that while ablation of the motor cortex produces only a slight impairment of the motor response, the additional removal of the premotor cortex leads to a complete abolition of that movement. The increased strength of stimulation elicits muscular contractions of a primitive character, terminating with more or less pronounced epileptic

seizures. Even a very high voltage of stimulation does not produce either pain or fear. Movements of the hindleg produced by strong stimulation may be due to the fact that hindleg area of the cortex was spared.

DISCUSSION

As seen from our results electrical stimulation of both the VL and VPL nucleus gives rise to isolated movements of the contralateral leg, provided that the parameters of stimulation are properly chosen. Why is it that only high frequencies (200—300 c/sec) of thalamic stimulation produce isolated movements of limbs is not clear, particularly if we take into account that the optimal frequencies of cortical stimulations are much lower. Thus, in the study of Tarnecki (1962a), in which the movements of the foreleg or the hindleg were elicited in waking cats by stimulation of the sensorimotor cortex, the frequency of 50 c/sec gave fluent and isolated responses, similar to those obtained in the present paper.

There are other striking differences between the effects of stimulation of the sensory cortex and the motor cortex on the one hand and the effects of stimulation of the VL and VPL nuclei on the other.

With regard to stimulation of the sensory cortex, to our best knowledge it is always emotionally indifferent, that is, it never has any nociceptive aspects. On the other hand, it was found by us that if the stimulation of the VPL nucleus is strong, the animal clearly shows the aversive response manifested both by typical local defensive flexion reflex and by emotional fear response. Moreover, the somesthetic sensations produced by VPL stimulation seem to be more durable than those produced by cortical stimulation, as judged from the long-lasting after-effect in the form of licking the leg, sniffing it, shaking movements, etc. It may be supposed that stimulation of the VPL nucleus throws into action some reverberating circuits which outlive the actual stimulation. Probably these reverberating loops are not activated by stimulation of the sensory cortex.

No less interesting is the comparison between the effects of stimulation of the motor cortex and stimulation of the VL nucleus. As is well known, stimulation of the motor cortex gives an abrupt lifting of the leg with very short latency and low threshold. On the other hand flexion of the leg produced by VL stimulation exhibits an exceedingly long latency, high threshold and very slow recruiting. Whereas stimulation of the motor cortex may be given with intervals of one minute or less without affecting the character of the response, VL stimulation

should be given once in 3—5 min, otherwise the response will deteriorate.

The problem of a long latency and very slow augmenting of VL produced movements is very difficult to understand. There is ample electrophysiological evidence to show that stimulation of the VL nucleus evokes a response in the pyramids after a latency of a few msec (Branch and Martin 1958, Amasian and Weiner 1966). Therefore one may ask why this stimulation does not exactly reproduce the cortical stimulation.

One possibility may be that repeated stimulation of the VL nucleus produces a potent recurrent inhibition of thalamic neurons, which blocks them for a length of time and then for some reasons becomes gradually removed (cf. Eccles 1966). If so, the question arises as to why the neurons of the VPL nucleus behave in a different way. It seems that electrophysiological experiments should answer that question.

To end the comparative analysis of the effects of cortical versus thalamic stimulations, it should be noted that whereas by stimulating the cortex (both motor and sensory) we can easily find points from which the movements of the hindleg are obtained, we were strikingly unsuccessful in this respect when stimulating the thalamus. The isolated hindleg movement was obtained only once by stimulating the VPL nucleus. The movements of the hindleg elicited by stimulation of the VL nucleus were never isolated, and we could not separate them from those of the fore leg.

Let us return now to the comparison of VL-induced movements with VPL-induced movements. Below we summarize once again their main differences:

The threshold of the VPL responses is lower than that of the VL responses, the latency shorter and the recruitment faster. The VPL responses have a clear somesthetic aspect, which is completely absent in VL responses. The aversive responses are more likely to occur with VPL than with VL stimulation. On the other hand, VPL responses are easily inhibited by other activities of the animal, such as locomotion or food intake, while VL responses are not.

Now we should discuss the effects of cortical lesions upon thalamogenic movements.

As was indicated above, stimulation of the VPL nucleus after the sensorimotor lesion fails to produce the isolated movement; however, an increase of the strength of stimulation leads to a general excitement of the animal of a clearly nociceptive character. This would suggest that the VPL nucleus contains not only relay neurons transmitting messages to the sensory cortex, but also those neurons which send messages to other cerebral structures. Whereas the former neurons are