Acta Biol. Exp. 1969, 29: 17—28

INSTRUMENTAL CONDITIONING OF THALAMOGENIC MOVEMENTS AND ITS DEPENDENCE ON THE CEREBRAL CORTEX

Remigiusz TARNECKI and Jerzy KONORSKI

Department of Neurophysiology, Nencki Institute of Experimental Biology, Poland

(Accepted Nevember 15, 1968)

In the previous paper (Tarnecki and Konorski 1969) it was found that high-frequency stimulation of the nucleus ventralis posterolateralis (VPL) and nucleus ventralis lateralis (VL) thalami produces in waking cats isolated movements of the contralateral limbs. In most instances lifting of the foreleg was observed.

In our earlier studies (Tarnecki 1962a, Tarnecki and Konorski 1963) we were concerned with the problem of instrumental alimentary conditioning of cortically induced movements. It has been established that movements of the hindleg are transformed into instrumental responses only in those cases in which they are elicited by stimulation of the sensory cortex, but not by stimulation of the motor cortex. It was concluded from this experiment that instrumental responses can be formed only from those movements which are initiated by stimuli impinging upon the afferent side of the nervous system.

The aim of the present experiments was twofold. First, it had to be established whether the movements produced by thalamic stimulation could be instrumentally conditioned. If so, the next problem arose concerning the role in instrumental conditioning of the cortical areas indispensable for the occurrence of the thalamogenic movements.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on 10 cats used in a preceding study (Tarnecki and Konorski 1969). The experimental box is represented in Fig. 1. On the right side of the box there was a feeder in which successive bowls were placed by an automatic device.

After the electrodes were implanted into the VPL and VL nuclei (see Tarnecki and Konorski 1969), and the optimal strength of electrical stimulation was selected for elicitation of an isolated movement of the limb, the daily experimental sessions ran as follows.

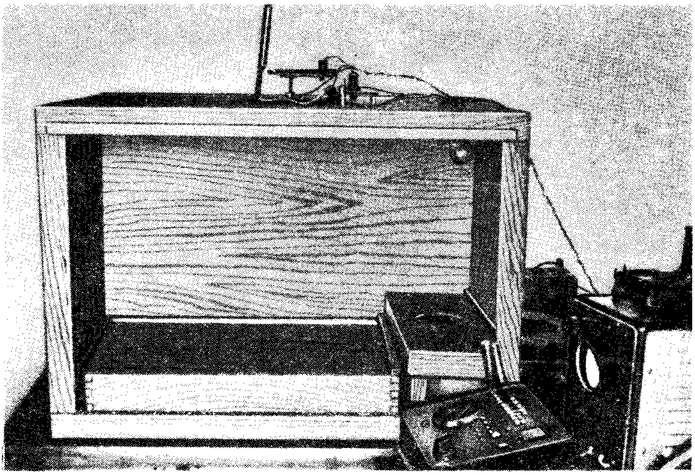

Fig. 1. Experimental box

The animal was placed in the box and electric stimulation was applied twenty times per session. When the cat performed the required movement in response to the stimulation, a bowl containing a piece of raw meat was put into position. The cat hearing the click of the moving bowl immediately approached the food and ate it. The intertrial intervals lasted 3—5 min.

When the cat started to perform active movements similar to those elicited by stimulation, they were immediately reinforced by food. Gradually their number increased so that stimulation was applied less frequently and eventually was completely withheld. Each session continued to consist of 20 reinforced trials irrespective whether the movement was elicited by stimulation, or was active.

When the training reached the stage in which the animal immediately after entering the box started to perform the instrumental movements and did so with regular frequency, a cortical operation was made in which the sensorimotor area, or sensorimotor and premotor area contralateral to the trained movement was removed. Two weeks after surgery the CR experiments were resumed and the instrumental responses were tested. After several weeks of retesting the cats were sacrificed and the anatomical examination of the brains was carried out (cf. Tarnecki and Konorski 1969).

RESULTS

Instrumental conditioning of VPL-evoked movements. The CR experiments were performed in five cats (no. 1, 2, 3, 7, 9). We present below the descriptions of training in each cat.

Cat no. 1. At first the cat was habituated to the experimental box and feeding procedure, and the optimal current of stimulation of the left VPL nucleus was chosen. It was found that stimulation with 300 c/sec, pulse rate 1 msec, and strength 3.2 v (0.2 ma) produced an isolated regular flexion of the right foreleg. After stimulation the animal often licked his forepaw.

Thereafter, the regular instrumental training began consisting in reinforcing with food every movement elicited by VPL stimulation. Already at the end of the first session the animal turned to the feeder immediately after stimulation was turned on even before performing the movement. At the end of the second session four active movements of the foreleg appeared. They were quite similar to those produced by stimulation.

In the following sessions the animal performed active movements only when a few stimulations of the VPL nucleus were given beforehand. We present below the protocol of the fourth session.

After coming to the box cat is sitting at the feeder for 5 min, looks at his right leg, puts his leg into the empty bowl. The further course of the session runs as follows:

No. of trial	Time	Stimulation		Movement	Food	Comments
1	5 min	300 c/sec	3.2 v	VPL-evoked	+	From trial 7 till the end of the session regular active movements of high amplitude are performed. Sometimes before performing the movement the cat licks his foreleg
2	8 min	300 c/sec	3.2 v	VPL-evoked	+	
3	8 min 20 sec	—	—	active	+	
4	9 min	—	—	active	+	
5	9 min 30 sec	—	—	active	+	
6	13 min	300 c/sec	3.2 v	VPL-evoked	+	
7	13 min 15 sec	—	—	active	+	
8	14 min	—	—	active	+	
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	.	.		.	.	
20	21 min 30 sec	—	—	active	+	

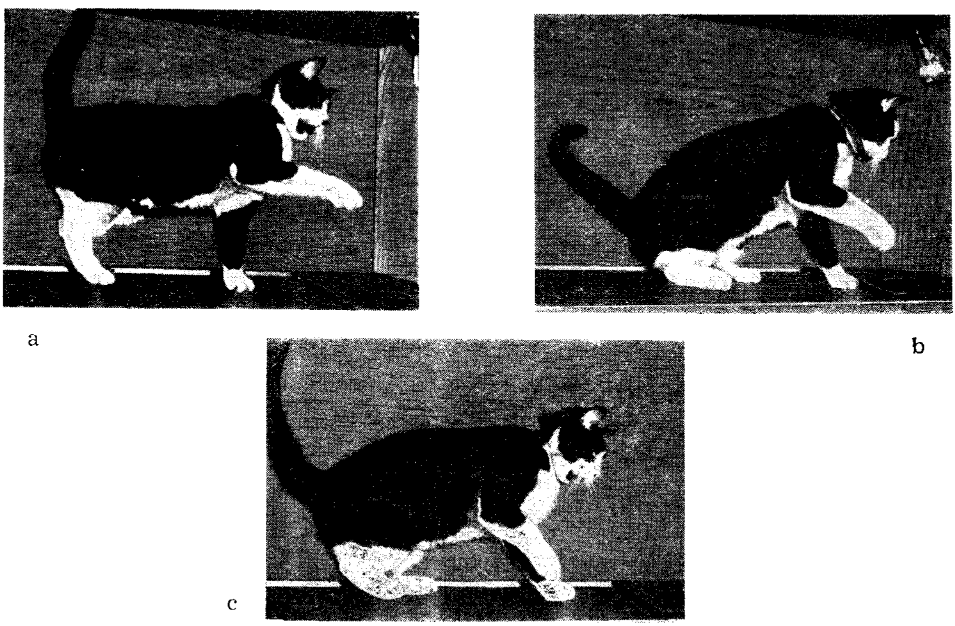
A similar picture is seen in the fifth and sixth session in which the performance of the active movements also had to be facilitated occasionally by VPL stimulation, particularly at the beginning of the session. It was observed, however, that the effective strength of current could be reduced to 2.0 v (0.12 ma). Beginning from the seventh session VPL-evoked movements were no longer needed, since the cat started to perform active movements soon after entering the box. Since the movements became regular and were performed immediately after the cat ate the preceding portion of food, the duration of the session (20 trials) was reduced to about 4 min, that is the instrumental responses were separated by about 12 sec.

It is worthwhile to note that when the instrumental reflex was firmly established the character of the motor response underwent some change. Whereas the response to stimulation consisted of a flexion of the leg in wrist, elbow and shoulder, the active movement in the later period of training consisted only in the flexion of the elbow. Interestingly, VPL stimulation produced in that period also the same simplified movement.

Cat no. 2. VPL stimulation, 300 c/sec, 4.5 v, evoked a quick and high lifting of the foreleg in the standing position with forward extension. After 12 trials stimulation was followed by approaching the feeder and expecting food. In the third session, after 7 stimulation trials (that is 67 trials in total), the active movements appeared which were identical to those produced by stimulation (Fig. 2a). In the fourth session the active movements appeared after two stimulation trials. From the fifth session stimulation was no longer needed, and the whole set of 20 movements was performed during 4—7 min.

From the twelfth session on, the character of the active movements was changed, because the cat began to perform them from the sitting position without extending the leg forward (Fig. 2b).

Cat no. 3. Stimulation of the VPL nucleus, 300 c/sec 3.0 v, produced a typical flexion of the foreleg performed in the sitting position. In the second session, when the current was turned on the animal became



a b c

Fig. 2. Instrumental conditioned responses in cat no. 2 in the early period (a), in a later period (b) and after removal of the sensorimotor cortex (c)

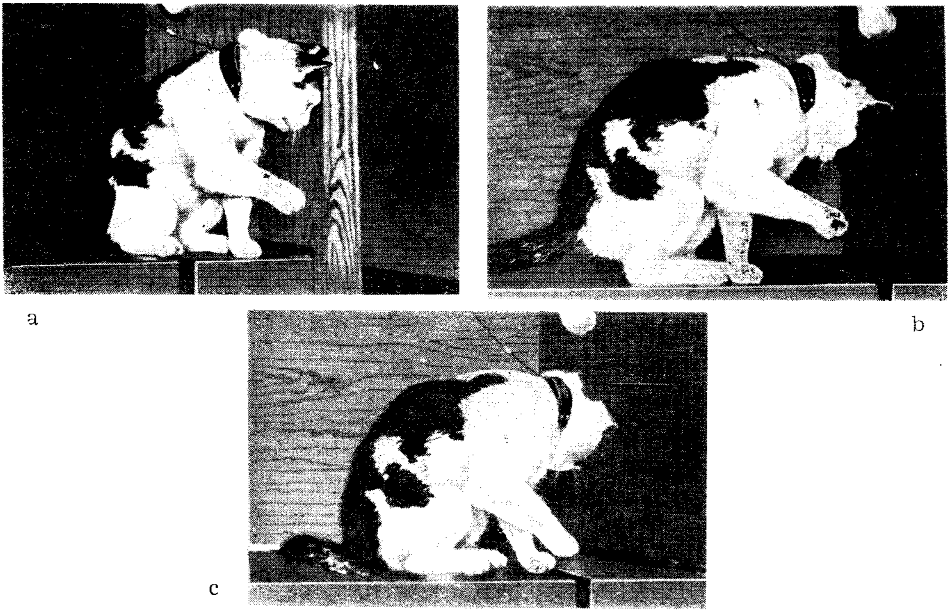


Fig. 3. VPL-induced movement (a), instrumental conditioned response (b) and instrumental response after removal of the sensorimotor cortex (c) in cat no. 9

disquiet, put his head into the empty bowl, sniffed the feeder or licked it. After six stimulation trials the cat, after having eaten his portion of food, began to lick his foreleg, lay down on the floor of the box, rolled for some time, then after a while returned to the sitting position. This bizarre behavior was repeated again and again during the second and third session. In the fourth session, after the forth trial (that is, after 64 stimulation trials in total) the active movements appeared which were quite similar to those produced by stimulation. As in cats no. 1 and 2 in subsequent two sessions the active movements followed a few stimulation trials. The effective strength of the current was reduced to 1.2 v.

From the seventh session active movements appeared as soon as the cat entered the box and stimulation was no longer needed. The animal performed his quota of 20 movements with reinforcement in about 4 min.

Cat no. 7. VPL stimulation, 300 c/sec, 5.0 v, evoked the movement of the hindleg performed in standing position.

After 14 trials the cat began to sniff the feeder and licked intensively his right hindleg or the right side of his body. When stimulation was turned on he became quiet, looked at the feeder, then got up and performed the movement. Sometimes when the movement was very small or absent, food was not presented and stimulation was turned off. Then the cat became disquiet and intensively licked his hindleg and body.

The first active movements appeared after 16 stimulation trials in the seventh session (136 trials in total). During six succeeding sessions active movements appeared always after a few stimulation trials, the threshold of stimulation being dramatically reduced: the current of only 1.0 v produced regular movements with short latency.

After 14 sessions the active movements became regular and were performed with maximal speed.

Cat no. 9. Stimulation by 300 c/sec, 3.5 v current produced a quick isolated movement of the fore leg consisting in its forward extension (Fig. 3a). After 7 stimulation trials in the third session the active movement appeared, which was an exact copy of the VPL produced movement (Fig. 3b). In the two following sessions the active movements had to be facilitated by movements elicited by stimulation. In the sixth session this facilitation was no longer needed.

Below we sum up the main characteristics of the instrumental training of VPL-evoked movements (Table I).

Table I

Main characteristies of the instrumental training of thalamogenic movements

No. of cat	Stimulation	Movement of the	Voltage applied	First session in which instrumental movement appears	Number of stimulation trials till the first instrumental movement appears	First session in which instrumental movement became stable
1	VPL	foreleg	3.2	second	36	seventh
2	VPL	foreleg	4.5	third	47	fifth
3	VPL	foreleg	3.0	fourth	64	seventh
7	VPL	hindleg	5.0	seventh	136	fourteenth
9	VPL	foreleg	3.5	third	47	sixth
5	VL	foreleg	5.0	fifth	93	sixth
8	VL	foreleg	6.0	fifth	93	sixth
10	VL	foreleg	7.0	seventh	130	eighth

1. In the first stage of conditioning the stimulation of the VPL nucleus — or, to put it more precisely, the somatic sensation produced by this stimulation — becomes a classical food CS manifested by the animal approaching the feeder, sniffing and licking the empty bowl,etc.

2. The instrumental movements of the foreleg appear after about 50 stimulation trials and those of the hindleg after 136 trials, but they do not occur regularly and must be preceded by thalamic stimulation. Only

in the further training is their rate increased and they appear immediately after the animal enters the box.

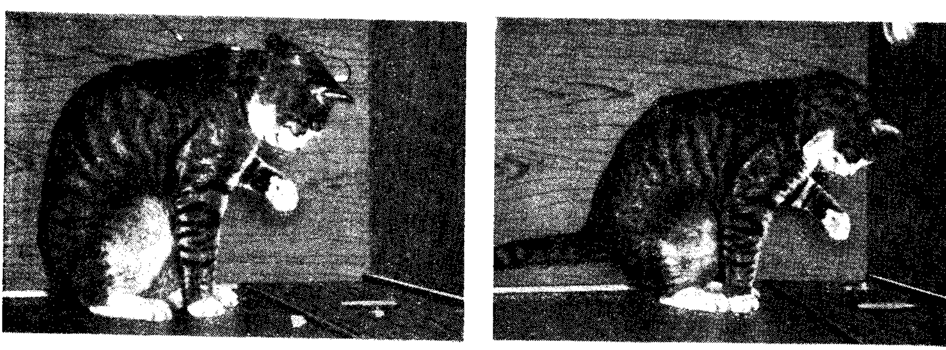
3. In the transitional period the threshold of thalamic stimulation evoking the movement is dramatically decreased.

4. With prolonged training the instrumental movement which initially completely mimics the VPL-evoked movement may become somewhat simplified.

5. In the early stage of instrumental conditioning the animal exhibits clear symptoms of sensory paresthesias of the contralateral leg and side of the body.

Instrumental conditioning of the VL-evoked movements. The experiments of this type were performed on three cats (no. 5, 8 and 10). Since the course of instrumental training was nearly identical in each cat, we present below its joint description (Table I).

Stimulation of the VL nucleus (300 c/sec, 5.0—7.0 v) elicited in all three cats a slow and gradual raising of the contralateral foreleg in extended position combined with supination (Fig. 4a). The latency was about 10 sec. After a number of stimulation trials (93, 93, 130 respecti-



a b

Fig. 4. VL-induced movement (a) and instrumental conditioned response (b) in cat no. 8

vely) the animals began to perform the active movements. In contradistinction to the VPL group, once the first active movements appeared, they were performed regularly and no facilitation by applying thalamic stimulation was needed. The shape of the movements was exactly the same as that in stimulation trials (Fig. 4b), except that their performance was swift and fluent and they did not possess a tonic and coerced character observed in VL-evoked movements. The movements did not undergo any changes till the end of training (about 30 sessions). The intervals between instrumental responses, which in the previous group were as short as about 15 sec, remained very long till the end of training and amounted to one or two minutes. It should be reminded that VL-evoked stimuli also required very long intervals, otherwise they became very poor or even failed to occur (Tarnecki and Konorski 1969).

The effects of cortical lesions on instrumental responses of the thalamic origin. After the CR training was completed, six animals (three of the VPL group and three of the VL group) were subjected to cortical operations. In three cats (no. 2, 7, 9) of the VPL group and one cat (no. 10) of the VL group, only the sensorimotor cortex was removed; in two other cats of the VL group (no. 5, 8) the sensorimotor cortex and the premotor cortex was ablated (see Tarnecki and Konorski 1969, Fig. 4 and 5).

Below we present short descriptions of the animals' CR performance after these operations.

Cat no. 2, VPL group. Movement of the foreleg. Sensorimotor lesion. The general motor efficiency was only slightly impaired and soon returned to normal. On the other hand, the instrumental responding was very strongly impaired. The amplitude of the movements was very small (Fig. 2c), and the intervals between responses were much prolonged. The fatiguability of the instrumental responses was so great that it was not possible to enforce a full quota of 20 movements per session from the animal.

After several weeks the instrumental responses became more regular and the cat was able to execute all the 20 movements in 20—24 min (before operation 4 min). The general character of the movements did not improve.

Cat no. 9, VPL group. Movement of the foreleg. Sensorimotor lesion. In spite of a very slight impairment of the general motor efficiency, the instrumental responding was very poor. The movements were small (Fig. 3c), irregular and prone to fatigue. After about 10—12 responses, the movements became so small that they were hardly recognizable as instrumental responses.

Cat no. 7, VPL group. Movement of the hindleg. Sensorimotor lesion. The CR performance was strongly deteriorated. The trained movements became so small that they were difficult to be identified. Strong fatiguability and very long intervals between responses.

Cat no. 10, VL group. Movement of the foreleg. Sensorimotor lesion. A few weeks after operation the animal's motor efficiency hardly differed from that before operation. His CR performance was, however, impaired. Although the animal was able to perform from time to time a movement of normal amplitude and shape, this occurred rarely, because of the conspicuous fatiguability.

Cat no. 5. VL group. Movement of the foreleg. Sensorimotor and premotor lesion. The general motor skill after operation was much worse than in the preceding cats. The animal crouched instead of walking and his motor coordination was very poor. He was not able to perform any manipulative movements. For four weeks after operation the instrumental CR was absent.

Thereafter the motor efficiency of the cat gradually improved, although it was still very poor. In that time the instrumental movements were restored but they were very low and irregular. This condition failed to change for several months.

Cat no. 8. VL group. Movement of the foreleg. Sensorimotor and premotor lesion. The general motor impairment, although prominent, was less severe than in cat no. 5. The instrumental CR was strongly impaired and was limited to a slight jerking up of the leg from the floor. Since the affected foreleg was generally hyperactive, it was sometimes difficult to identify a movement as a true instrumental response.

In sum the CR performance after the cortical lesions may be characterized as follows. Although in all our cats the instrumental CRs were preserved, their amplitude was very small and they were readily fatiguable. The general motor efficiency was much more strongly affected after sensorimotor and premotor lesions than after pure sensorimotor lesions. Similarly, the instrumental CRs were still poorer after the larger lesions than after the smaller ones.

DISCUSSION

Two findings reported in this paper should be discussed. One is the instrumentalization of the thalamogenic movements, the other, the survival of the instrumental CR after destruction of the cortical area intervening in the occurrence of those movements.

The ready instrumentalization of the VPL-evoked movements is easy to understand. In the preceding paper (Tarnecki and Konorski 1969) it was pointed out that stimulation of the VPL nucleus mimics the sensory peripheral stimulation of the noxious or subnoxious character of the limb concerned, stimulation producing the flexion reflex. According to the general rules of instrumental conditioning discussed elsewhere (Konorski 1967) this flexion reflex under proper reinforcement is easily transformed into an instrumental CR.

Further features of the instrumental CR derived from VPL-evoked movements fully confirm this thesis. It was found that in early stages of instrumental training active movements are facilitated by VPL-evoked movements. Conversely, the latter movements are now elicited by a much lower strength of current than before training. These facts are easily explained by the assumption that some center intervening in the performance of the VPL-evoked movement plays an active role in conditioning. For, after the CR is established, this center is activated both by the "unconditioned" stimulus applied to the VPL nucleus, and by the conditioned stimulus represented by the experimental situation. In consequence, there is a mutual facilitation between the responses deriving from those two sources. The fact that the instrumental conditioned response exactly imitates the VPL-evoked movement, at least in the first stage of conditioning, also speaks in favor of that assumption.

Another curious phenomenon observed in the early stages of the instrumental training should be commented upon. As follows from our protocols, in the first experimental sessions the cats show signs of paresthesia of the side of the body contralateral to the VPL electrodes. This paresthesia observed in the intertrial intervals is manifested by the cat licking his paw, rubbing the body against the wall, etc. These phenomena strongly support a hypothesis claiming the formation of connections between the center of the given drive (here hunger drive) and the center of the stimulus provoking the trained movement (Jankowska and Sołtysik 1960, cf. also Konorski 1967, Chapter XI). It should be added that all the features characteristic of instrumental conditioning of the VPL-evoked movements are also observed in instrumental conditioning of "natural" responses such as scratch reflex.

Instrumental conditioning of VL-evoked movements follows a somewhat different course than that of VPL-evoked movements. It is true that the shape of the instrumental movement is an exact copy of the VL-evoked movement, but whereas the latter is performed very slowly, the instrumental movements are prompt and fluent, as if the recruitment were not needed for their occurrence. On the other hand, the trained movements do not follow each other with maximal frequency (as is the case with all other instrumental responses known to us), but are separated by intervals of more than one minute. No paresthesias of the body are seen in the intertrial intervals and the once established instrumental response does not need any facilitation. Certainly all these features are connected with the fact that the mechanism of the VL-provoked movement is different from that of the VPL-provoked movement, but we are far from a clear understanding of this mechanism.

Let us turn now to the second major finding described in this paper, namely that of the partial preservation of the instrumental response after the ablation of the sensorimotor cortex and even after the ablation of the sensorimotor and premotor cortex. This result is even more puzzling if we take into account that these lesions completely abolish the thalamogenic response from which the instrumental response takes its origin.

In previous works of this laboratory it was established that when a relatively simple motor response is instrumentalized, it is strikingly resistant to the damage sustained to the nervous system. We know that even extensive lesions sustained to the cerebral cortex (Jankowska and Górska 1960, Stępień et al. 1961), afferent pathways (Jankowska 1959, Górska and Jankowska 1961, Tarnecki 1962b), thalamic nuclei (Tarnecki 1962c, 1963) and efferent pathways (Górska 1967, Górska et al. 1966a, b) do not abolish the instrumental response although they impair it to a greater or lesser extent.

The same is true of instrumental movements derived from thalamic stimulation. Although after cortical lesions these movements become simplified or even abortive, there is no doubt that they are the remnants of instrumental responses. What the structures controlling these responses are is not clear without further experimentation.

SUMMARY

1. Movements of the limbs evoked by electrical stimulation of the VPL nucleus or VL nucleus with the frequency of 300 c/sec were used in instrumental alimentary conditioning in cats.

2. The VPL-evoked movements were instrumentalized after about 50 trials for the foreleg and after 136 trials (one cat) for the hindleg. In the first stage of conditioning there was mutual facilitation between the instrumental movements and the VPL-evoked movements, consisting in triggering of the instrumental movements by VPL-evoked movements on the one hand, and in lowering the threshold of the VPL-evoked movements by instrumental conditioning on the other. After the instrumental CR was firmly established the animals performed the trained movement immediately after eating food presented after the preceding movement.

3. The VL-evoked movements were instrumentalized after about 100 trials (for the forelimb). When instrumental conditioning was completed, the intervals between the performances of the trained movement remained long, amounting to one minute or more.

4. The instrumental responses transformed from the thalamogenic responses have exactly the same shape as the former ones.

5. Lesions sustained in the sensorimotor and premotor cortex do not abolish the instrumental responses derived from thalamic stimulation, but make them low, irregular and fatiguable.

This study was partly supported by Foreign Research Agreement No. 287 707 of U. S. Department of Health, Education and Welfare under PL 480.

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