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INSTRUMENTAL CONDITIONED REFLEXES ELABORATED BY MEANS OF DIRECT STIMULATION OF THE MOTOR CORTEX

R. TARNECKI, J. KONORSKI

Department of Neurophysiology, Institute of Experimental Biology, Warsaw

According to the statement put forward long ago by Konorski and Miller (1933, 1936), if in a given situation, or in the presence of a definite sporadic stimulus, a particular motor act is evoked *in any way* and reinforced by food, while the situation or the stimulus itself is not, then after a number of such trials the animal starts to perform this motor act "actively", i. e. in the absence of those factors by which it was originally elicited.

According to the way by which the movements are produced they can be divided into three following groups:

1. The movement can be produced as an effect of any unconditioned or conditioned reflex. Here we shall classify both such movements which are elicited by definite, specially administered stimuli, as for instance lifting of the leg in response to an electric shock, scratch movements produced by putting a piece of cotton wool into the ear, etc., and such movements which are executed accidentally in a given situation, as for instance lying down or getting up, barking, coming to a definite place of the room, etc. These last movements, generally denoted as "spontaneous", may be of course also considered as effects of reflexes elicited by some hidden stimuli.

2. The given movement can also be produced as the effect of passive displacement of the body, for instance passive bending of the leg, passive putting the leg on some platform, etc. Of course some of the passive movements may also comprise a reflex element: in fact, compulsory bending of the animal's leg may elicit proprioceptive reflexes described long ago by Sherrington (1909) as so-called lengthening and shortening reactions. The problem, whether the passive displacement itself, or the reflex which is elicited by it, is the basis of the formation of an instrumental conditioned reflex, is a matter for discussion. According to Konorski and Miller's (1933, 1936) hypothesis the essential part in the elaboration of an instrumental reflex is played by proprioceptive stimuli being reinforced by food, i. e. by mere displacement of the leg generating these stimuli. On the other hand Woodbury (1942) criticized this view pointing out that the performance of a movement plays a decisive role here (see later).

3. At last, the movement may be produced by artificial stimulation of some

Fig. 1. A cat with implanted electrodes.

central structures controlling its performance, e. g. by electrical stimulation of definite points of the motor cortex.

The first two methods were used as a means for the elaboration of instrumental conditioned reflexes by all authors dealing with those reflexes. On the other hand, the method of using electrical stimulation of the cortex with this aim has so far been applied only exceptionally. Indeed, so far as we know, it was applied only long ago by Loucks (1936) and by Konorski and Lubińska (1939). Since the methods used by these authors were rather inadequate, we thought that the problem should be reinvestigated by applying a modern and more perfect method of implanted electrodes. Particularly, we had in view the question whether the instrumental response established by this means represents a precise copy of the movement induced by cortical stimulation, and whether the destruction of the stimulated point after the elaboration of the instrumental reflex would lead to its abolition.

The experiments were performed on cats. The technique of implanting electrodes was similar to that applied by Sheatz and will be described in detail elsewhere (Fig. 1). Several electrodes were placed on the surface of the cortex with dura mater intact. Stimulation of the respective points produced the movements of contralateral foreleg or hindleg. Rectangular pulses of 50cps frequency, 1 msec duration, and 2—5 V in strength were used. The animal was put in an experimental cage of $70 \times 50 \times 50$ cm (Fig. 2), and after a period of habituation a given point of the cortex was electrically stimulated; after the movement was elicited it was immediately reinforced by presentation of a piece of meat from the foodtray. Such trials were repeated at irregular intervals of 1—5 minutes. When the animal started to perform spontaneously the movement analogous to that produced by

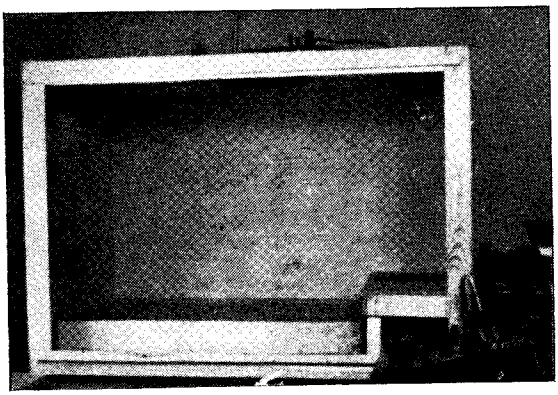

Fig. 2. The experimental cage.

stimulation, it was also reinforced. When such an instrumental conditioned reflex became firmly established, stimulation of the cortex was altogether discontinued. Usually about 30 trials were given in each experimental session. After the experiments were terminated the location of electrodes was verified by electrocoagulation.

The experiments in which the flexion of the foreleg was trained in this manner were performed in 17 animals. The stimulating electrodes were placed either on the motor area just behind the cruciate sulcus, or in the sensory area near the ansate sulcus (Fig. 3, circles). In all the cats the instrumental conditioned reflex was elaborated very easily. Already in the first experiment (after 5—15 trials) the animal started to perform the movement of the foreleg actively, and in a few successive experiments the reflex became firmly established. Usually in the second or third experiment the stimulation of the cortex had to be applied at the beginning of the session, in following experiments, however, the animal started to perform the movement spontaneously from the very beginning and did so with maximal frequency (Fig. 4A, B.).

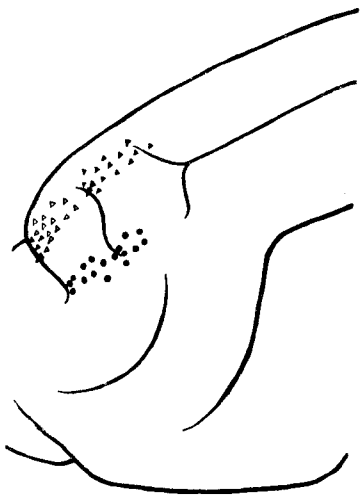

Fig. 3. The location of electrodes on the cortical surface of experimental animals. Circles, points whose stimulation produced foreleg movements; triangles, points whose stimulation produced hindleg movements. Full circles and triangles denote those points from which instrumental reflexes have been established; open triangles denote those points from which instrumental reflex could not be elaborated.

The character of the movement in some cases was quite similar to that observed with the cortical stimulation; sometimes, however, it underwent a definite evolution, namely became more "natural". This happened particularly in those cases in which the motor area was stimulated and the evoked movement had a rather unusual character.

The training of the instrumental reflex involving the hindleg was carried out originally in 26 animals. Much to our surprise it was found that in 17 cases the instrumental reflex could not be established in spite of the fact that electrical stimulation of the cortex produced a very high and isolated flexion of the hind limb. In other cases the instrumental reflex was established quite easily, more or less in the same way as it was in those experiments in which the movement of the foreleg was elicited (Fig. 4C, D).

The analysis of our experimental material has shown that the instrumental conditioned reflex failed to be established in those cases in which the electrode was placed just behind the cruciate sulcus, i. e. in the motor area for the

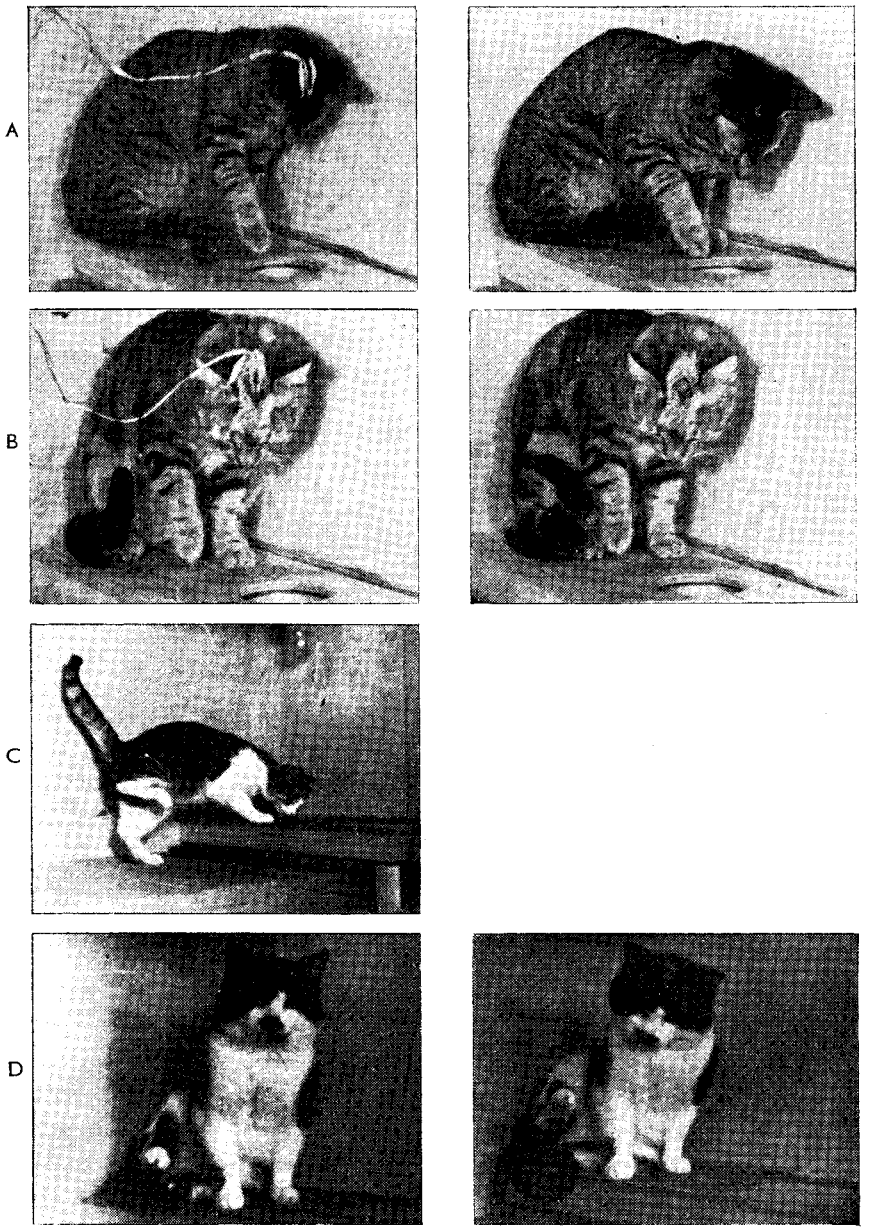

Fig. 4. The movements elicited as the effect of cortical stimulation (left) and instrumental reflex (right), A, movement of the foreleg produced by stimulation of the motor area. B, movement of the foreleg produced by stimulation of the sensory area. C, movement of the hindleg produced by stimulation of the motor area. D, movement of the hindleg produced by stimulation of the sensory area. Note the "artificial" character of the movement in A: the leg is flexed in shoulder and elbow, but extended in wrist. Also note that in spite of very high amplitude of the movement in C, the instrumental reflex could not be established.

hindleg (Fig. 3, open triangles). In all these cases the voltage of stimulation necessary to provoke the movement was relatively low (about 2V), the movement had a short latency, it grew rapidly and attained a high amplitude. With the cessation of stimulation the movement was abruptly discontinued.

On the other hand the movements produced by stimulation of the sensory area (Fig. 3, full triangles) required a great voltage (up to 4V), they increased more slowly, they did not stop immediately after the cessation of stimulation, and they were not so isolated as in the first case.

Although the movements brought about by stimulation of the sensory cortex were usually lower than those produced by stimulation of the motor cortex, they became very easily instrumentalized in contrast to the movements produced by stimulation of the motor hindleg area, which could not be instrumentalized at all.

In order to test whether this analysis was correct, experiments with 10 additional cats were undertaken. Electrodes were placed both in the motor and sensory area for the hindleg. In 5 cats the cortical points situated in the sensory area were stimulated and the respective movement of the hindleg was reinforced by food. After a few days the instrumental conditioned reflex was established in the usual way. In the other 5 cats stimulation of the motor area was first applied. In spite of 30 experiments with 24 trials each, the elicitation of the hindleg movement by this stimulation, followed by food reinforcement, did not lead to the elaboration of the instrumental reflex. However, this reflex was easily established when stimulation of the sensory area was applied.

The results so far obtained throw some new light upon the mechanism of elaboration of instrumental conditioned reflexes. First K o n o r s k i and M i l l e r' s thesis that movements produced in any way become instrumental by food reinforcement is probably not true, since the movement of the hindleg produced by stimulation of the motor cortex fails to be instrumentalized. If we assume that the movement produced by stimulation of the sensory cortex, in contrast to that produced by stimulation of the motor cortex, has a reflex character, the conclusion seems to be plausible that only those movements may become instrumental which are brought about by the reflex route, i. e. belong to group 1 of movements specified above. This conclusion seems also to solve the above mentioned controversy concerning the elaboration of instrumental conditioned reflexes by utilizing the passive movements (movements group 2). Indeed, since we accept that only reflex movements can become instrumentalized, it follows that elaboration of the instrumental conditioned reflex in this case is due to the proprioceptive reflex participating in the passive movement, and not to the passive displacement of the limb itself.

The problem arises why the principle established for the reflexes involving the movements of the hindleg does not hold in the case of foreleg reflexes. Two possibilities may here be proposed. One is that the sensory area for the foreleg

is larger than is generally believed and partially overlaps the motor area. The second possibility is that the movements of the foreleg in cats are so much more instrumentalized in the animal's life, that a movement produced in any way may be easily transformed into a natural movement already established as instrumental reaction connected with securing food. Which of these suppositions is right should be elucidated by further experiments.

According to the evidence collected in our laboratory, the elaboration of instrumental conditioned reflexes is due to the formation of conditioned connections between the centres of conditioned stimuli and the centres of particular "drives" on the one hand, and definite motor centres on the other (Wyrwicka 1952, Konorski 1960, Sołtysik 1960). It is now seen that this thesis should be somewhat modified. It appears that it is not motor centres themselves which take a direct part in conditioned connections, but rather some other centres which lie in between sensory and motor centres engaged in the given motor acts. The problem where these centres are to be looked for is a matter of future investigation.

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