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NEUROPHYSIOLOGY

Instrumental Conditioned Reflexes after Section of the Pyramids in Cats

by

T. GÓRSKA, E. JANKOWSKA and M. MOSSAKOWSKI

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Recent literature suggests that voluntary movements are not so closely connected with the pyramidal system as was previously assumed. For example, some clinical data show that after a unilateral section of the pyramidal tract patients are able to perform purposeful movements, even in the distal parts of the affected extremities [1]. On the other hand, experiments with sensori-motor cortex ablations in cats [3], [4] and dogs [2], [5] have shown that various instrumental conditioned reflexes (CR) are disturbed to various degrees by the same cortical lesion: while some of the CR swere relatively unimpaired after this operation, others were greatly depressed. In view of these facts it seemed interesting to investigate the effect of pyramidotomy on various instrumental CR's.

Material and methods

The effects of uni- and bilateral pyramidotomy on instrumental food CRs established before operation were studied in 42 cats. According to their origin, the instrumental CRs could be divided into two groups, three reflexes in each group.

The instrumental CRs of the first group were derived from the reaction of stretching out the forepaw to reach the food which was inaccessible by mouth. The following reflexes are included in this group: a) placing one forelimb on a platform, b) pressing a button inside a semicircular screen, c) pushing a button in a horizontal tube (Fig. 1, a—c). At the beginning of training the appropriate movements were evoked in the experimental situation by presenting a piece of meat in such a way (e.g., on the button or inside the tube) that the animals had to perform the required movement in attempting to reach it, whereupon the regular food reinforcement was offered in the food-tray. After some time, the animals learned to perform the given movement without any direct baiting.

Instrumental CRs of the second group were derived from specific unconditioned motor reactions: scratching movements of the hindlimb, lifting the hindlimb as for cleaning the anal region and rubbing the cheek with the forelimb. At the beginning of the training the respective unconditioned reflexes were evoked in the experimental situation by specific stimuli (putting cotton into the ear, applying adhesive to the anal region and the cheek), and each such movement was immediately followed by food. After a few days of such procedure the stimuli eliciting the respective unconditioned reflexes could be withdrawn because the animals began to perform nearly identical movements

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as soon as they were brought to the experimental situation. In the Fig. 1a, b, c the instrumental "scratching" (d), "cleaning" (e), and "rubbing" (f) CRs are illustrated.

Each experimental session consisted of 20 reinforced performances of the trained movement. Depending on the quality of the task, the instrumental responses began to appear after 2—8 sessions and the training was continued for an additional 15—20 sessions until the character of the instrumental CRs became stable. The frequency and the amplitude of the motor acts were recorded, as well as their characteristic properties. Each of the reflexes described above was trained in 8—12 animals, and most of the cats learned to perform 2 out of the 6 instrumental reflexes — usually one from each group. These reflexes were trained in different experimental situations.

The pyramids were sectioned in the medulla, at the level of the trapezoid body. Only those animals in which complete destruction of the pyramids was histologically verified are included. The postoperative state of the reflexes was examined once or twice a week, beginning from 1-2 weeks after the operation when the animals had recovered, and was followed for 2-3 months. During the time of postoperative observation, not only movements identical with those of the preoperative period, but also less perfect responses were reinforced in order to avoid extinction of the CRs.

Results

The pyramidotomy affected the two groups of CRs differently. All the CRs of the first group were undoubtedly preserved in all operated cats, both after uniand bilateral pyramidotomy. Their amplitude was practically unchanged, but their frequency was diminished by 25–50 per cent. As far as the quality of the movements is concerned, they were much less precise than before operation. This was particularly true of button-pressing and button-pushing CRs. After unilateral operation the button-pressing movements were usually performed after a few unsuccessful attempts; after the bilateral operation the cats in most cases simply placed the limb near the button without attempting to press it. In button-pushing CR both the uni- and bilaterally pyramidotomized cats merely touched the horizontal tube, but they could not insert the paw into it and push the button.

The reflexes of the second group were much more seriously impaired. After a bilateral pyramidotomy the CRs disappeared almost completely in all the cats and did not reappear during the time of postoperative examination. The results of unilateral sections were less uniform. Rubbing-the-cheek CR disappeared in all the cats but one, while the scratching CRs was preserved in half of the animals and cleaning CR was present to some extent in all of them. However, the conditioned responses were very small and of low frequency.

In order to clarify the difference between the effect of pyramidotomy on the CRs of the first and the second group, the thresholds of the motor reactions from which the instrumental reflexes were originally derived were also examined. A marked rise in the thresholds of the unconditioned scratching, cleaning and rubbing reactions was found in the operated animals as compared to normal ones. On the contrary, the reaction of stretching out a forepaw for food, tested in a situation where no precise movements were needed, was evoked in the operated animals as easily as in intact ones.

Discussion

In the light of the results described above two main problems should be commented upon. The first question concerns the possible sources of differences between the effects of pyramidotomy on the two groups of instrumental CRs, the second concerns the mechanism by which the pyramidal system can influence voluntary behaviour. For the sake of clarity, we shall restrict our discussion to voluntary movements consisting of a coarse and global motor acts of one of the limb, such as all the reflexes of the second group, and the movements of placing the limb on a platform as well as stretching it towards the button in the case of the CRs of the first group.

As seen from our results, the pyramidal system does not play an identical role in respect to all instrumental CRs. All the reflexes classified to our first group appeared to be relatively independent of the pyramidal system, while all the reflexes classified to the second group seemed to be dependent on the integrity of this structure. These differences seem to be mainly related to the character of responses from which these two groups of instrumental CRs were originally derived. Whereas the CRs of the second group were derived from definite spinal reflexes, the CRs of the first group were based on a response whose reflex arc and character are as yet undefined. It is possible that the reaction of stretching out a forepaw is a primitive voluntary response, acquired early in the ontogenesis and dependent on the integrity of some extrapyramidal structures. The second source of differences may be related to the kind of stimulation used to establish the instrumental CRs in both groups. In the case of the CRs of the second group, cutaneous stimuli were used to evoke the respective unconditioned reflexes, whereas in the CRs of the first group visual stimulation may have played an important role. It is possible, therefore, that pyramidotomy selectively affects only those instrumental CRs which are based on somatosensory input and does not influence the instrumental responses based on visual input.

The existence of a correlation between the impairment of the CRs of the second group and the increase in thresholds of the corresponding unconditioned reflexes strongly suggests that a center of an unconditioned reaction is also involved in the instrumental CR arc. The disappearance of the instrumental CRs of the second group after pyramidotomy might be thus interpreted as due to a decrease in the level of excitability of some elements in the reflex arc of the corresponding unconditioned reaction. This explanation is supported by electrophysiological data showing that the pyramidal tract exerts a facilitatory influence on spinal reflex arcs [6]. It is possible, therefore, that the changes in voluntary behaviour after pyramidotomy are brought about to some extent by, or partly reflect, the changes in unconditioned responses, which under normal conditions are also influenced by the pyramidal system.

DEPARTMENT OF NEUROPHYSIOLOGY, NENCKI INSTITUTE OF EXPERIMENTAL BIOLOGY, POLISH ACADEMY OF SCIENCES (ZAKŁAD NEUROFIZJOLOGII, INSTYTUT BIOLOGII DOŚWIADCZALNEJ IM. M. NENCKIEGO, PAN)

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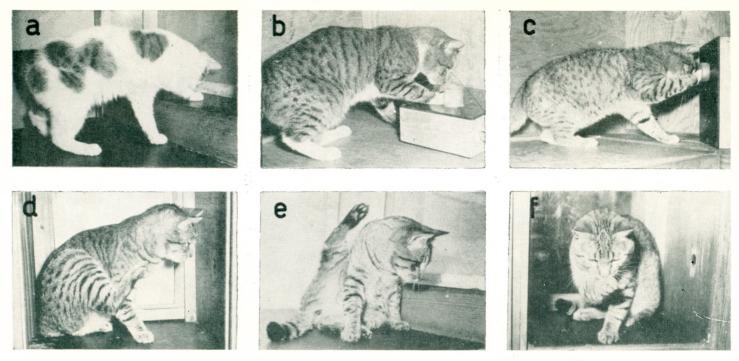
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Photographs of instrum ental CR's: a) placing a limb on a platform, b) button-pressing, c) buttonpushing, d) scratching of the ear, e) cleaning of the anal region, f) rubbing of the cheek.

Photographs a-c are taken from bilaterally pyramidotomized cats, photographs d-f from normal animals

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