VARIABILITY OF THE CROSSED EXTENSOR REFLEX (PHILIPPSON REFLEX)

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Tonic contraction of limb muscles depends on stimulation not only of their "own" proprioceptors but also of receptors of the musculature of the contralateral limb [4]. It was shown in a previous work that in decerebrate animals the crossed reflex elicited by stretching the quadriceps (Philippson's reflex) was the usual feature, and also that contraction of the contralateral extensors could occur in conjunction with its own extensor reflex and with autogenic inhibition of the muscle being stretched [3]. A question that arises is whether stretching of the quadriceps invariably exerts an excitatory effect on the nervous centers of the contralateral limb extensors. There are data indicating that the tonus of the contralateral extensors under such circumstances can not only remain unenhanced, but even be depressed [7, 8]. In the present experiments a number of cases of "inversion" of the crossed extensor reflex has been observed. Presentation of data concerning the variability of this reflex forms the substance of this communication.

METHODS

Experiments were performed on 67 decerebrate cats. The animals were placed back down on the stand, the thigh bones were fixed by means of screws in the vertical postion. Tonically contracted quadriceps muscles maintained the shins in a position of some extension depending on the extent of decerebrate rigidity. If the angle between the femur and the shin was about 90° decerebrate rigidity was considered moderate. Stretching of one of the heads of the quadriceps was achieved by passive flexion of the limb at the knee joint. The shins were connected with isotonic myographs which under these conditions recorded changes in the length of the quadriceps muscles. On all the kymograms extension at the knee joint corresponds to a downward deflection. In a number of experiments a simultaneous record of the quadriceps electromyogram was made with the help of a two-channel cathode oscillograph. Needle electrodes with an inter-electrode distance of approximately 2 cm were used.

RESULTS

The crossed extensor reflex was obtained in individual decerebrate cats with unequal ease and was of different magnitude. In some cases this reflex became apparent with slight flexion of the limb (by 5-20° in the angle of the femur and shin), while in other cases it could only be elicited on full flexion or several repeat flexions of the limb. In the majority of cases the distinctive features in the Philippson reflex were associated with the extent of the decerebrate rigidity of the hind limb extensors. The reflex could be most easily elicited and had the largest magnitude in animals exhibiting moderate decerebrate rigidity (Fig. 1, b). The reflex was, as a rule, diminished (Fig. 1, a) in animals with slight rigidity. The reflex could not be elicited in preparations with very weak tonus of the extensors.

In a number of preparations (7 of 67) with weak and unstable decerebrate rigidity not only diminution but also inversion of the crossed extensor reflex was observed. When the limb was lightly passively flexed

(100-200 g) the tonus of the contralateral quadriceps was diminished as the result of which the shin was lowered somewhat. There was simultaneous weakening of the electric potentials of this muscle. If flexion of the limb was stopped, the contralateral shin returned to the original position. On increasing the passive flexion, however, inhibition of the crossed extensor tonus was replaced by its increase and the Philippson reflex was obtained. The

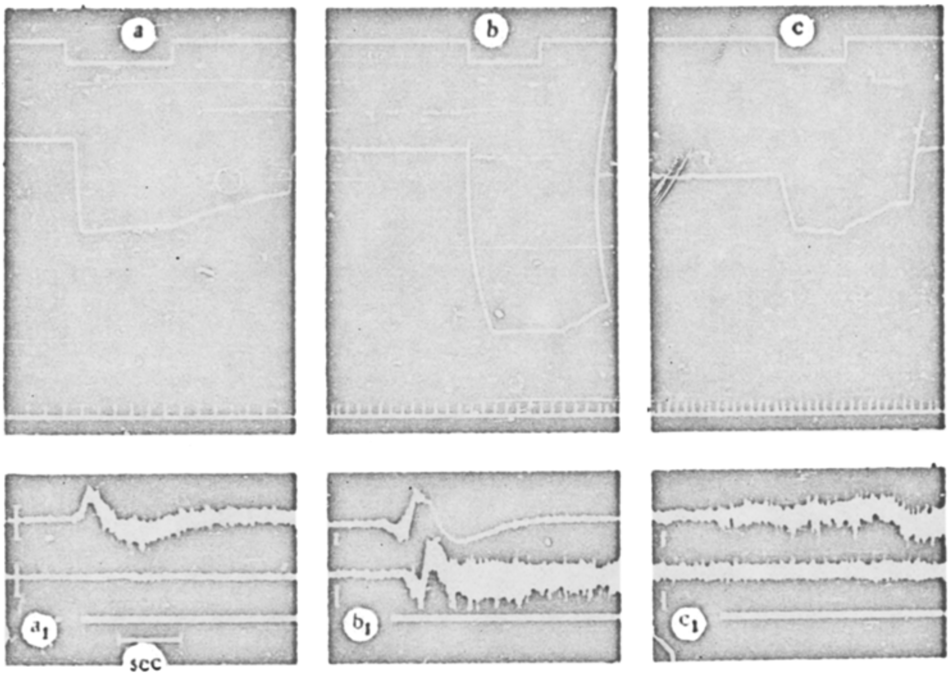

Fig. 1. Relation of the magnitude of the Philippson reflex and the extent of decerebrate rigidity. a) weak rigidity (angle between femur and shin 70°); b) moderate rigidity (90°); c) marked rigidity (125°).
Records from above down: a), b), c) stimulus marker, movements of right shin, time marker (1 second); a_1), b_1), c_1), electromyograms of the left and right quadriceps muscles, stimulus marker (passive flexion of the left limb). Calibration in all EMG records – 50 μ V.

reaction thus consisted of two successive phases. A typical example of such a response is given in Fig. 2, a.

In some experiments in which the two-phase form of the crossed extensor reflex was observed even the relatively weak stretching of the quadriceps muscle by the weight of the shin supported by it exerted an inhibitory effect on the centers for the contralateral extensors (2 cases). Termination of this stretching by slight passive extension of the limb led not to the usual gradual relaxation of tonus [3] but to a rapid contraction of the contralateral quadriceps muscle. In the case presented in Fig. 2, b, it was sufficient to raise the left shin slightly for the right limb to become extended (angle around 30°) and "freeze" in the new position.

The Philippson reflex proved to be weakened in preparations with very marked decerebrate rigidity (Fig. 1, c). It might have been supposed that a decrease in the amplitude of the reflex in these cases was connected with considerable degree of extension of the limb as a consequence of decerebration. However, not only the mechanical but also the electric reaction of the contralateral quadriceps muscle proved to be weak. As in cases of weak rigidity, so in the case of a background of very strong rigidity several instances of relaxation instead of contraction of the extensors of the contralateral limb were observed (5 cases). Inhibition of crossed extensors under these conditions, however, showed substantial differences from the form described above. In the first place, relaxation of the contralateral extensors occurred only on strong flexion of the limb (requiring 1-2 kg); in the second place, on increasing the flexion, relaxation of the contralateral quadriceps muscle was never seen to be replaced by its contraction. Inhibition of tonus in this case was also accompanied by depression of electric activity (Fig. 3).

Inhibitory forms of the crossed extensor reflex were detected particularly frequently on prolonged

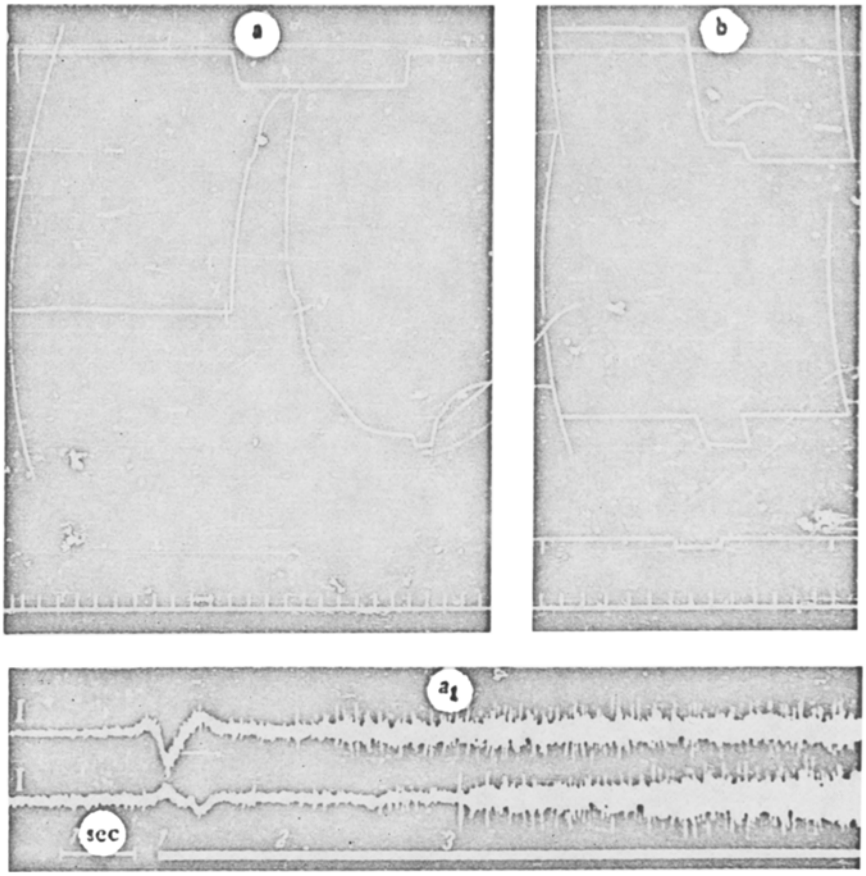

Fig. 2. Two-phase form of crossed extensor reflex against the background of weak decerebrate rigidity.
Records: a), a_1) – as in Fig. 1. Stimulus – gradual flexion of the left limb; figures indicate corresponding moments; records from above down: b) movements of the right shin, movements of the left shin, stimulus marker (gentle extension of the left limb), time marker (2 seconds). Knee flexors on the left are denervated.

observation, lasting several hours. It was then possible to establish how, in the same preparation, the character of the reflex reaction by contralateral extensors underwent changes with alterations in the extent of decerebrate rigidity. For example, at the beginning of an experiment decerebrate rigidity was moderate and flexion of the limb at the knee elicited the Philippson reflex. Later the tonus of the extensors gradually diminished and after approximately one hour the same stimulation elicited the two-phase form of the reflex. After another 1½ hours rigidity of the preparation became very weak with the appearance of continuous rhythmic movements of the hind limbs which interfered with observations. Intracranial tampons were changed and the experiment interrupted for one hour. During this time the decerebrate rigidity became very strong (angle between femur and shin 140°). At this stage, instead of the former reactions strong flexion of the limb elicited considerable diminution in the tonus of the contralateral extensors with no signs of its increase.

Comparison of the effects of flexion of opposite limbs revealed the possibility of asymmetry in the resulting crossed extensor reflexes. If, for example, flexion of the left limb resulted in relaxation of the contralateral extensors, flexion of the right limb could result in Philippson's reflex.

The method used for the stretching of the quadriceps muscle did not exclude the possibility of "collateral" (skin, joint) stimulation. Control observations were therefore carried out in which a number of nerve trunks were sectioned (sciatic nerve above the separation of the deep thigh branches, n. saphenus, obturator nerve) and novocaine anesthesia applied to those areas of the skin whose receptors could have been stimulated on passive flexion of the limb. Both inhibitory forms of the crossed extensor reflex were observed under these conditions also.

These data support the suggestion that the main cause of inhibition of the tonus of the contralateral extensors was stimulation of the quadriceps muscle proprioceptors on stretching of the muscle (it is true that denervation of the knee joint in these experiments was not complete; the medial articular twig from the femoral nerve was preserved). Reflex flexion of the contralateral limb was associated with relaxation of the quadriceps muscle (not with contraction of the flexors). This follows from the fact that these forms of reflex reactions were fully apparent after denervation of the knee joint flexors in the limb on which the crossed reflex was being observed and also from electromyographic data.

It must also be noted that inversion of the crossed extensor reflex takes place especially frequently with impairment of the "effector" quadriceps muscle. In experiments (performed with a different aim in view) in which the muscle twigs of the femoral nerve were dissected the inhibitory forms of the crossed extensor reflex were encountered in approximately half the cases (3 of 6 experiments).

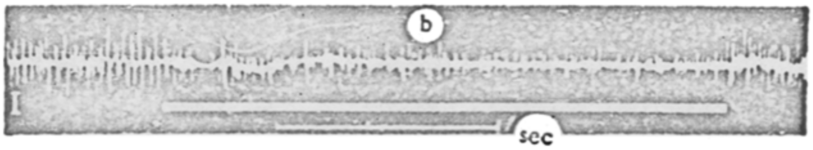

Fig. 3. Inhibitory form of crossed extensor reflex with strong decerebrate rigidity. Records from above down: a) movements of right shin, stimulus marker (passive flexion of left limb), time marker (1 second); b) simultaneously recorded EMG of the right quadriceps muscle.

Adequate stimulation of the quadriceps muscle proprioceptors can thus produce not only an excitatory but also an inhibitory effect on the centers of crossed extensors. The crossed extensors reflex posseses a variability similar to that which is well-known in the case of antagonist-muscle contractions in the course of exteroceptive reflexes [2, 6, 1]. The data obtained are difficult to interpret from the point of view of constant values of afferent impulses and nerve fibers conducting them. Although in the majority of preparations any supra-threshold stretching of the quadriceps muscle elicited contraction of the contralateral extensors, in other preparations the same stimulation elicited opposite reactions. Evidently, the basic factors which determine the variability of the crossed extensor reflex are changes in the functional state of the nerve centers. This is suggested by the dependence of the course of this reflex on the intensiveness of decerebrate rigidity and the degree of muscle stretching, the occurence of different forms of the reflex in the same preparation, and the significance of the state of the effector part of the reflex arc (observations on preparations with damaged muscle).

In decerebrate preparations the distinctive features shown by the course of spino-cerebral reflexes depend on the activity of the reflex apparatus in the preserved parts of the brain. It may be supposed that variability of simple unconditioned motor reflexes represents a phenomenon which constantly accompanies coordination of complex movements under conditions of normal reflex activity, with "reflexes and reflex apparatus of the lower levels being used for the achievement of reflex actions of higher levels" (Ukhtomsky, Vol. 5, p. 230).

SUMMARY

Stretching of one of the quadriceps was caused by flexion of one of the limbs of decerebrate cats. Variations of the length and the electromyogram of the quadriceps were recorded. The amplitude of the Philippson reflex was most at medial decerebration rigidity. The Philippson reflex was lowered both in cases of very strong and weak rigidity; in some experiments it was even inhibited. In case of flaccid rigidity the tonus of the contralateral extensors was lowered by gentle flexion of the limb (100-200 g) and then enhanced by forced flexion. In cases of strong rigidity inhibition of crossed extensors was caused only by strong flexion (1-2 kg). The crossed extensor reflex is variable just as the reflex of antagonistic muscles during exteroceptive stimulation.

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