

MOTOR RESPONSES TO STIMULATION OF
THE RED NUCLEUS IN CATS

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Motor effects evoked by stimulation of the red nucleus through implanted electrodes were studied in six cats with unrestricted behavior. A single stimulus applied to the red nucleus evoked local contraction of the flexor muscles of the contralateral limb. Two subcortical stimuli applied to the red nucleus at an interval of 5-40 msec evoked a summation effect, expressed as a motor response of the corresponding limb. Depending on the location of the electrode, local contractions of the forelimb or of the hind limb only could be evoked. If two subthreshold stimuli were applied simultaneously to the opposite nuclei, a summation effect was evoked but only if homologous areas of the nuclei were stimulated; this result is evidence of a somatotopic organization of rubrospinal projections. Repetitive stimulation lasting not more than 1 sec did not evoke a response of attention to the flexing limb.

The rubrospinal system plays an important role in the mechanisms of coordinated motor activity. Electrophysiological methods have been used to study the influence of the red nucleus on spinal motoneuronal activity [2-4, 6, 7, 9, 10, 17].

The influence of the red nucleus on combined motor responses and on the animal's behavior has received much less study. Data on this problem in the literature are contradictory. Some workers [9] have observed local limb movements in response to stimulation of the red nucleus in the cat without any change in behavior; others [5] observed only shaking movements of the animal in response to stimulation of the red nucleus. Meanwhile Delgado [8] describes complex behavioral acts evoked by stimulation of this structure in monkeys.

The object of the investigation described below was to study motor responses in cats to stimulation of the red nucleus and with no restriction on behavior.

EXPERIMENTAL METHOD

Chronic experiments were carried out on six cats with bipolar electrodes implanted into the red nucleus. In four animals the electrodes were inserted bilaterally, so that the number of observations on responses to stimulation of the red nucleus could be increased and the character of interaction between the two structures could be investigated.

Single pulses of current (0.5-1 mA, 1 msec) or a series of pulses of the same duration with a frequency of 200 Hz, applied for 10-100 msec were used for stimulation. Besides visual observations and motion pictures, mechanographic recordings of the movements were produced. The animal's position during recording was not restricted. After the end of the experiments the location of the electrodes was verified histologically. The experimental technique was described in detail previously [1].

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EXPERIMENTAL RESULTS

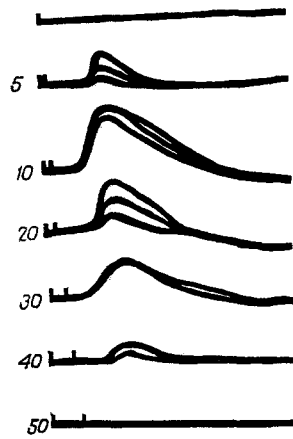


Fig. 1. Mechanogram of forelimb during summation of two subthreshold stimuli applied to the red nucleus. Top curve, single subthreshold stimulus. Numbers on left denote interval between stimuli (in msec).

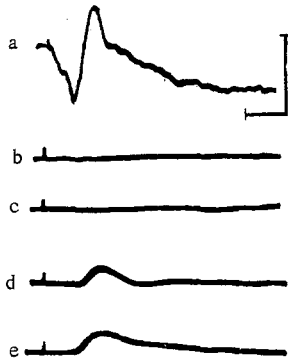


Fig. 2. Effect of summation during simultaneous subthreshold stimulation of homologous points of the two red nuclei: a) evoked potential in right nucleus in response to stimulation of left (calibration: 5 msec, 250 μ V); b,c) mechanograms of right and left forelimbs respectively in response to application of subthreshold stimuli at different times; d,e) mechanograms of forelimbs during simultaneous stimulation of both nuclei.

In response to application of a single stimulus to the red nucleus a weak contraction of one or several flexor muscles took place. These responses developed on the contralateral side only. Extension of contralateral or ipsilateral limbs was not observed in any of these animals. This fact confirms data in the literature on the production of EPSPs in flexor motoneurons and IPSPs in extensor motoneurons of the contralateral side in response to stimulation of the rubro-spinal system [2, 6, 18]. Repetitive stimulation of the red nucleus evoked much stronger motor responses. The strength of contraction of muscles hitherto responding to single stimuli was increased and other flexor muscles of that same limb became participants in the response. For example, if a single stimulus evoked flexion of the hand only, the more proximal portions became involved in the response to repetitive stimulation, including muscles of the shoulder girdle. Repetitive stimulation evoked extension of both forelimbs in one animal, accompanied by lifting of the head and anterior parts of the trunk, i.e., a response very similar to that described by Jung and Hassler [11] to stimulation of the red nucleus took place. However, as the histological control showed, the stimulating electrode in this animal was in the reticular formation close to the red nucleus. It was therefore excluded from the general observations.

Despite the fact that repetitive stimulation evoked well-marked motor effects, as a rule the experimental animals paid no attention to the flexing limb, and after the end of stimulation they resumed their original pose.

Stronger motor responses were observed to the first few stimuli, and sometimes they were more generalized in character. Despite this, however, the shaking of the animal was not so well-marked in response to stimulation of the red nucleus as it was to stimulation of the somatosensory areas of the cortex [1]. If the stimuli were repeated at a frequency of not more than once every 3-5 sec, the movements gradually became more local and they persisted throughout the experiment if the animal did not alter its posture.

The thresholds for evoking motor activity varied with the position of the animal's body. The highest threshold was observed when the original tone of the flexor muscles was lowered, for example, if the cat was sitting in a usual position, supported on the forelimbs. If two subthreshold stimuli were applied, muscular contractions were observed only if the interval between them did not exceed 40 msec (Fig. 1). The maximal summation effect occurred, however, if the interval between the subthreshold stimuli was 10-20 msec.

Isolated flexion of a single forelimb or hind limb in response to threshold stimulation could not be obtained in every case. Nevertheless, in two animals flexion of the contralateral forelimb only, and in two others local contractions of the muscles of the hind limb only were observed. In one of the animals a single threshold stimulation of both the right and the left red nucleus evoked flexion of the hand on the corresponding sides. In response to application of subthreshold stimuli at different times no motor response occurred (Fig. 2) with either the right or the left limb, and only an evoked focal potential developed in one nucleus in response to subthreshold (for muscular contraction) stimulation of the other nucleus. In response to simul-

taneous stimulation of both nuclei a summation phenomenon took place, manifested as flexion of one or the other limb. No such summation effect was observed in the other animals in which stimulation of one nucleus evoked flexion of the limb while stimulation of the other nucleus evoked a motor response of the hind limb. These facts are in good agreement with the results of anatomical [14, 17] and physiological [12, 15, 16, 19] investigations which showed a somatotopic organization of the rubrospinal tract. Evoked potentials arising in one red nucleus in response to stimulation of the other and with a short latent period confirm the anatomical evidence for the existence of direct connections between the nuclei [13]. The presence of these bilateral rubro-rubral connections suggests that the summation effect observed during subthreshold bilateral stimulation of the nuclei may arise through interaction between afferent and efferent impulses actually in these structures. The possibility of interaction between rubro-fugal volleys on spinal interneurons likewise cannot be ruled out. Afferent impulses traveling along rubro-rubral connections can evoke focal responses to stimulation of the opposite nucleus. However, activation of the red nucleus by means of an afferent volley never evoked the motor responses which appeared to direct stimulation of that nucleus.

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