Effects of Locus Coeruleus Stimulation on Neuronal Activities in the Rat Superior Colliculus*

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Summary In urethane-anesthetized rats, effects of locus coeruleus stimulation on spontaneous and photically evoked discharges of superior collicular neurons were studied. In any layer of the superior colliculus the inhibited neurons were more numerous than the facilitated ones, and the latter increased relative to the former from the superficial to the deep layer.

Key Words: locus coeruleus, superior colliculus.

The investigation of the neuronal activities in the cerebellum (HOFFER *et al.*, 1973) and hippocampus (SEGAL and BLOOM, 1974) has revealed that the noradrenergic projection system of the locus coeruleus (LC) exerts an inhibitory action on target neurons. Recently it was found, however, that the noradrenergic control from the LC differed in nature according to species of neurons receiving it; in the dorsal lateral geniculate nucleus, relay neurons were excited while interneurons were inhibited when noradrenaline was applied iontophoretically or electrical stimulation was given to the LC (ROGAWSKI and AGHAJANIAN, 1980a, b; KAYAMA *et al.*, 1982).

Neurons in the superior colliculus (SC) can be classified into several groups according to their locations in the SC and functions (FUKUDA *et al.*, 1978b). The present study was therefore made to examine how LC stimulation differentially affects activities of the classified neurons of the SC.

LC stimulation was successfully examined in 98 SC neurons in urethane-anesthetized rats (8-12 weeks old), some of which were immobilized by gallamine and ventilated artificially. Details of the method for positioning a stimulating electrode in the LC and the criteria for classifying SC neurons are described elsewhere (FUKUDA *et al.*, 1978b; KAYAMA, *et al.*, 1982). To drive SC neurons photically, a light spot was turned on and off at the center of receptive fields

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plotted on a tangent screen (FUKUDA *et al.*, 1979). The LC was stimulated with trained square pulses of 0.05 msec duration from several seconds to several tens of seconds. They were 2–5 V at 200 Hz or 8–15 V at 20 Hz.

Single shock stimulation of the optic chiasm elicited in the SC a field response whose shape was specific to the depths of the recording site, and unit activities could be recorded simultaneously with the field response (FUKUDA *et al.*, 1978a, b). Thus, with the shape of the response it was easy to judge from what layers neurons were recorded. In this way the neurons recorded in the SC were divided into the following 3 groups; 1) neurons in the upper visual layer (stratum zonale and upper half of st. griseum superficiale; zone of horizontal cells (LANGER and LUND, 1974)), 2) neurons in the lower visual layer (lower half of st. griseum superficiale and st. opticum; zone of vertical cells (LANGER and LUND, 1974)), and 3) neurons in the deep, non-visual layer (st. griseum intermediale, album intermediale et griseum profundum).

With only a few exceptions, spontaneous discharges of SC neurons were either facilitated or inhibited by LC stimulation. The change of spontaneous discharges occurred with a latency of several seconds to several tens of seconds and became gradually manifest while the stimulation was continued. In Fig. 1, A, B, and D are sample records for the LC-induced inhibition, being distinguished from each other by the rapidity of the decrease of the discharge frequency. Record C, a typical example for the facilitation of spontaneous discharges, was obtained from the same electrode track as for record D with the same parameters of LC stimulation. It is suggested that excitation of the same group of LC neurons caused facilitation in one group of SC neurons and inhibition in the other. Whether LC stimulation caused facilitation or inhibition of spontaneous discharges, changes in the discharge frequency outlasted the stimulation by varying times not shorter than 10 sec.

In neurons recorded from the visual layer, effects of LC stimulation were tested upon photically evoked responses as well. The effects were either facilitatory or inhibitory on both of on- and off-responses. Records E and F of Fig. 1 are sample records for inhibition and facilitation of the photically evoked response, respectively. In E, while LC was stimulated, the photically evoked responses were reduced in the peak discharge frequency and made less sustained. In F, the photically evoked responses were affected by LC stimulation in a way virtually opposite to that in E.

When the visual layer units were exhibiting the spontaneous discharges, the latter were usually affected by LC stimulation in qualitatively the same way as the photically evoked discharge. In some neurons the spontaneous discharges were inhibited more rapidly and severely than the photically evoked responses, so that the response became more conspicuous against the suppressed background. This may be the phenomenon described as "signal-to-noise ratio improvement" by MOISES *et al.* (1981). As for neurons exhibiting facilitation of the photically

Fig. 1. Effects of LC stimulation on spontaneous discharges of 4 neurons (A, B, C, and D) and on visual responses of 2 neurons (E and F). Integrated discharge rate per sec (A to D) or per 0.5 sec (E and F) is shown in the ordinate. Stimulation periods are shown by thick horizontal bars under each record. For neurons A, LC stimulation was tested 3 times; in the third trial the stimulus intensity was reduced to 2/3 of the intensity in the first and second ones. Neuron A was recorded in the upper visual layer, neurons B, C, E, and F in the lower visual layer, and neuron D in the non-visual layer. Neurons C and D were recorded in the same electrode track and tested with LC stimulation of the same parameters. In E and F, responses were evoked by turning a light spot on and off at the center of a receptive field (upswings of trains of square waves indicate light-on periods).

evoked responses due to LC stimulation, no good examples could be obtained for the signal-to-noise ratio improvement.

By testing the effects of LC stimulation upon the spontaneous discharges in many SC neurons of various layers, it was found that the ratio of the incidence of neurons exhibiting facilitation to those showing inhibition differed according to the layers in which the neurons were located. As shown in Table 1-I, the ratio of the facilitated neurons to the inhibited ones increases as one passes through the SC from superficial to deep. The same tendency can be found with regard to the effects on the photically evoked responses (Table 1-II).

The present experiment has shown that the noradrenergic control from the LC is either facilitatory or inhibitory on SC neurons. Although attempts were

Table 1. The number of neurons affected by LC stimulation.

Layer	Inhibited	Facilitated	No effect	Total
I. Spontaneous discharges				
Upper visual	9 (90%)	1 (10%)	0	10
Lower visual	25 (64%)	7 (18%)	7 (18%)	39
Non-visual	14 (58%)	8 (33%)	2 (8%)	24
II. Visual responses				
Upper visual	3 (75%)	0	1 (25%)	4
Lower visual	15 (60%)	4 (16%)	6 (24%)	25

made to reveal the relation between the neuronal species and the nature of noradrenergic control exerted upon them, such remained unsuccessful. Instead, it was established that although in any layer of SC the inhibitory effect was more frequently observed than the facilitatory one, the ratio of the facilitated neurons to the inhibited ones increased from the upper to the lower visual layer and further to the deep, non-visual layer. The physiological meaning of such surface-to-depth gradient of the probability of SC neurons for receiving facilitation or inhibition from the LC remains to be clarified in future experiments.

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