UNEQUAL EFFECTS OF DIFFERENT PARTS OF THE CAUDATE NUCLEUS ON SENSOMOTOR CORTICAL UNIT ACTIVITY

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Evoked responses of sensomotor cortical neurons to stimulation of certain parts of the caudate nucleus were recorded in acute experiments on unanesthetized cats. Stimulation of the body of the nucleus proved to be less effective than stimulation of its head and was less frequently followed by facilitatory or inhibitory responses. Usually cortical unit activity was inhibited in response to stimulation of the ventral part of the head, and the index of inhibition was higher than in response to stimulation of the dorsal part. The absence of correlation between the caudate effects and responses to stimulation of the internal capsule evidently means that this difference cannot be attributed to involvement of capsular fibers.

One of the most important structures of the forebrain, the caudate nucleus, has a cellular structure which is fairly homogeneous throughout. For this reason some workers, when interpreting their results, sometimes do not attach importance to the part of the nucleus in which stimulating or recording electrodes are situated. However, sufficient evidence has now been obtained to show the functional heterogeneity of this formation [5-8, 15].

An important physiological feature of the corpus striatum is its ability to affect movement control. This property is effected largely through a change in the activity of the neocortical motor areas. It was therefore decided to study the influence of different regions of the caudate nucleus on neocortical single unit activity.

EXPERIMENTAL METHOD

Experiments were carried out on 28 unanesthetized, curarized cats. The technique of dissection and of recording cortical unit activity was described previously [1]. To stimulate the different parts of the caudate nucleus, 3 or 4 bipolar electrodes were inserted into it so as to correspond in the frontal and sagittal planes to coordinates given in the atlas [12]. A multiple electrode consisting of a series of (7 or 8) monopolar electrodes fixed to a common vertical trunk at intervals of 1 or 1.5 mm was used in 4 experiments. It was usually possible to pass such an electrode through the longest transverse diameter of the head of the caudate nucleus (Fig. 1). The ratio between the frequency of unit activity in response to stimulation and its spontaneous frequency was used as the index of inhibition or facilitation.

EXPERIMENTAL RESULTS

Activity of 185 sensomotor cortical neurons located in the zone of representation of the forelimb and predominantly at the depth of layers IV and V of the cortex was studied. The cell responses were evoked by stimulation of the caudate nucleus itself and also of the neighboring zone of the internal capsule at different frequencies (from 2 to 30/sec).

Caudate Responses. The cortical neurons responded differently to stimulation of different points of the caudate nucleus at the same frequency (Fig. 1). The character and intensity of the single unit responses

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TABLE 1. Responses of Sensomotor Cortical Neurons to Stimulation (3/sec) of Various Parts of the Caudate Nucleus

Type of response	Head								Body	
	medial sector		lateral sector		dorsal sector		ventral sector			
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Excitation . . .	6	12	7	9	7	17	4	9	5	16
Inhibition . . .	32	68	52	69	27	66	32	78	15	48
No response . . .	10	20	17	22	7	17	5	13	11	36

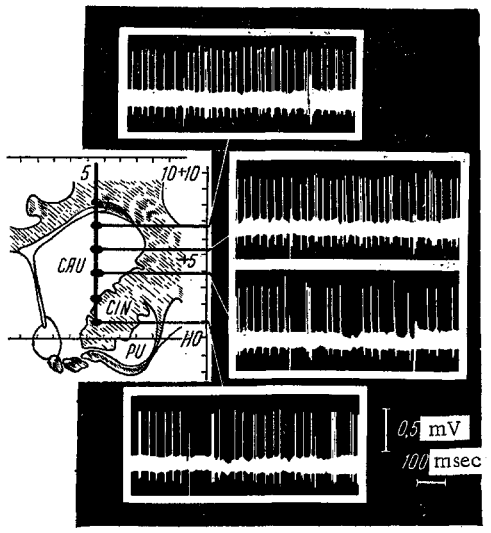

Fig. 1. Effect of stimulation of different points of the caudate nucleus on activity of the same neuron in the sensomotor cortex. Diagram taken from atlas [12] shows frontal brain section at F = 16 mm and localization of multiple electrode. CAU) caudate nucleus; CIN) internal capsule; PU) putamen. Remainder of explanation in text.

varied considerably from different points and at first glance without any regular pattern. Their responses could be similar, but at times the pattern was varied: inhibition was combined with facilitation or with no effect.

Altogether 112 points of the caudate nucleus were investigated. The results for 3 types of cell responses evoked by low-frequency stimulation are summarized in Table 1. Both a steady decrease of unit activity and responses with an inhibitory pause are classed as inhibition. The results for the ventral and dorsal zones of the head of the nucleus were obtained with the multiple electrode.

If these facts are compared, the appreciable predominance of inhibitory responses to stimulation of all parts of the nucleus will be noted, in agreement with earlier observations [2]. The effectiveness of stimulation of the medial and lateral sectors of the head did not differ significantly. Compared with them the body less frequently gave inhibitory responses and many neurons (twice as many as during stimulation of the head) did not respond to caudate stimuli. This confirms the view that the role of the body in the regulation of motor activity is more limited [6].

A marked difference was found when the character of the responses from the dorsal and ventral zones of the head was compared. In the latter case inhibition of unit discharges was particularly frequent, with a corresponding decrease in the incidence of areactive units. Conversely, the dorsal sector much more frequently gave facilitatory responses. Their appreciably higher frequency than in response to stimulation of the medial and lateral sectors of the same dorsal portion can probably be attributed to the use of monopolar stimulation. The essence of the situation, however, is something else – other conditions being equal, inhibitory responses were more numerous from the ventral zones of the head.

Two of these zones of the caudate nucleus differed not only in their relative proportion of facilitatory and inhibitory responses, but also in their unequal degree of inhibition. A previous investigation [2] showed that during low-frequency stimulation (2-5/sec) inhibitory responses usually were unstable, and the mean depression of spike activity was 20-30%. The use of a higher frequency of stimulation (10/sec) led to increased stability and intensity of inhibition. This frequency was accordingly used to compare the indices of inhibition for the dorsal and ventral portions of the head. Expressed as percentages they were 32 and 50%, respectively, ($P < 0.01$; Fig. 2).

According to previous observations [2], cortical neurons with different levels of initial activity differed in their sensitivity to caudate inhibitory influences. With an increase in the spontaneous firing rate, as a rule, the inhibitability of the cells decreased. In the present investigation the dorsal and ventral zones of the head were compared with respect to this criterion. The results showed that for neurons with a low

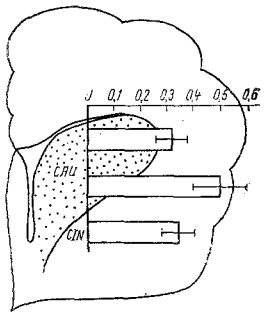

Fig. 2. Differences in intensity of inhibition of cortical neurons during stimulation of certain zones of the head of the caudate nucleus and internal capsule. Columns represent mean values of index of inhibition (complete inhibition taken as 1) with confidence limits.

initial firing rate (less than 12/sec) the mean index of inhibition for single stimulation of the dorsal zone was 0.34, while cells from the ventral zone were inhibited more strongly (0.5). However, because of the considerable scatter of the results the shift was not statistically significant ($P > 0.05$). For units with a high spontaneous firing rate (above 12/sec), however, the mean indices were not appreciably different (0.26 for the dorsal zone, 0.28 for the ventral).

The facts described above thus indicate some degree of functional heterogeneity of the head of the caudate nucleus: its ventral portions inhibited sensomotor cortical unit activity more frequently and strongly than the dorsal portions. This conclusion is in agreement with observations made by other workers [10, 14] who found a particularly sharp inhibition of cortically evoked movements during stimulation of the rostro-basal and baso-lateral regions of the head. Stimulation of the dorsal sectors, on the other hand, did not give this effect. The question arises: is this difference purely caudate in origin or is the increased strength of inhibition due to involvement of neighboring brain structures? As the electrode is moved in the dorso-ventral direction, it moves steadily closer to the internal capsule. Since some workers [9, 13] are inclined to explain many caudate effects by the looping of the current to fibers passing through the caudate nucleus, this problem requires special investigation.

Capsular Responses. During stimulation of the internal capsule (8 points only) different types of unit responses, outwardly similar to the caudate responses, were observed. However, as a previous investigation [4] showed, if the electrodes were located in the capsule or in the boundary zones of the caudate nucleus, the total number of inhibitory responses did not increase, but actually fell. Comparison of the intensity of inhibition during stimulation of the capsule and of different parts of the head (Fig. 2) likewise leads to the conclusion that the responses of the ventral portion cannot be attributed to the spread of current to capsular fibers. Finally, the types of cell responses evoked in an experiment by two electrodes located side by side were compared: one electrode was in the ventral portion of the head, the other in the internal capsule. These experiments showed that neither the direction nor the intensity of the capsular effects correlated with caudate effects. Meanwhile, two neighboring points of the caudate nucleus were most frequently characterized by shifts in the same direction.

A regular pattern was detected only for inhibitory pauses in the unit responses. Their mean duration during capsular stimulation was higher than those recorded from the ventral parts of the head (144 and 100 msec, respectively). The inhibitory postsynaptic potentials arising in sensomotor neurons during stimulation of the nucleus [11] may thus be, at least in part, capsular in origin. This may explain the resistance of the caudate inhibitory pauses (up to 160 msec in duration) to amphetamine, which can inhibit the function of the caudate nucleus [3].

The heterogeneity of the head of the caudate nucleus is thus probably not attributable to involvement of the internal capsule, but it is most likely the result of the character of organization of the neostriatum itself.

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