INVESTIGATION OF NEURONAL CONNECTIONS IN
THE DORSOCAUDAL TEGMENTUM OF THE CAT
BY A MICROSTIMULATION METHOD

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Unit responses in the caudal part of the tegmentum were investigated by a microstimulation method in the mesencephalic cat. The thresholds of appearance of direct and synaptic responses with latencies of 0.8-1.4 and 1.1-2.0 msec were found to depend on the distance from the electrode to the cell recorded. Responses with a low threshold (0.2-1.1 μV) were found much more often in neurons located 6.3-7.0 mm from the surface of the inferior colliculus than in more dorsal or more ventral zones. The relationship between the threshold I, in μA, of the direct response of the low-threshold cells and their distance r, in μ, from the stimulating electrode is approximated satisfactorily by the equation \[ I = 3.3 \times 10^{-4} r^{1.8} + 0.2 \]. The curve of I as a function of r for synaptic responses is usually more sloping and it has minima for responses recorded not near the cell. The index of synaptic response of some cells rose with an increase in the frequency of stimulation to 20-60/sec.

INTRODUCTION

High-frequency stimulation of a localized region in the dorsodorsal part of the tegmentum induces locomotion of the mesencephalic cat in acute experiments and in cats with bilateral destruction of the centrum medianum and nucleus parafascicularis or the subthalamic region of Waller [15] in chronic experiments [3]. This "locomotor" region of the mesencephalon corresponds in its topography to the nucleus cuneiformis [6, 10]. Its stereotaxic coordinates (after Horsley-Clark) are P 1.5-2.0, L 3.5-4.0, and H 0.0 (--0.5). Interaction between neurons in the caudal tegmentum could not be detected by correlation analysis [8]. Just as in the rostral tegmentum [9], the times of spike generation by two neurons (about 1 mm apart) were independent.

The object of this investigation was to study the organization of connections in the caudal tegmentum by a microstimulation method [12-14]. The relationship between the thresholds of the direct and synaptic responses and the distance between the extracellular electrode recording the unit response and the electrode through which the stimulus was applied was investigated.

METHOD

Tracheotomy, ligation of the common carotid arteries, and precolliecular postmammillary decerebration [5, 6, 11] were carried out under ether anesthesia [5, 6, 11]. The cat's head was fixed in a stereotaxic apparatus. The temperature was maintained at 37.0-37.5°C. The experiment began 1-2 h after stopping the anesthetic. Activity was recorded and stimulation applied through glass pipets (tip 3-10 μ in diameter) filled with Wood's alloy and coated electrolytically with platinum black. The two electrodes were arranged parallel under the microscope so that the distance between their tips in the plane perpendicular to their axes was 10-40 μ. The two electrodes were inserted perpendicularly by means of a common micromanipulator into the dorsodorsal part of the tegmentum (Horsley-Clark coordinates P 1.5-2.5, L 3.5-4.0, H 1.0 (--3.0)). The stimulating electrode could be moved upward or downward relative to the recording electrode by means of a second micromanipulator.
Fig. 1. Characteristics of direct responses and histograms of latent periods of synaptic responses of different neurons (a–e): a) amplitude, $A$, of action potential as a function of location of recording electrode (direct response); b) threshold of direct response, $I$, and amplitude $A$, of action potential as a function of location of recording electrode; c, d) histograms of latent periods of early ($r = 10 \mu m$, $N = 285$) and late ($r = 200 \mu m$, $N = 115$) synaptic responses; e) threshold of direct response as a function of stimulus duration.

Action potentials of single neurons were recorded after preamplification from the screen of a cathode-ray oscilloscope. Square pulses (0.1 msec) of negative polarity were used as stimuli. The negative pulse was followed by a positive pulse 0.01 msec in duration, reducing the duration of the artifact. The neurons were identified during stimulation at 2-4/sec with a current of 3 $\mu$A when the tips of the recording and stimulating electrodes were at the same depth, or with a current of 20 $\mu$A when the vertical distance between the electrode tips was 300 $\mu$. Some cells had spontaneous activity. Responses of 46 neurons (direct from 32, synaptic from 34) were studied in 12 experiments.

RESULTS

The amplitude of the extracellular action potentials was 0.1-1.0 mV. It was reduced by half from its maximal level by a change of 30-50 $\mu$m in the position of the recording electrode. The error in determination of the location of the neuron relative to the electrode tip could be of that magnitude (Fig. 1a).

Direct Responses. The response threshold for a vertical distance $r$ between the tips of the stimulating and recording electrodes was taken to be the strength of current $I$ inducing action potential generation in 4-6 of 10 cases when stimuli were applied at a frequency of 1.5/sec (index of response 0.4-0.6). The value of $r$ was changed (25-μ steps) by raising ($+r$) and then lowering ($-r$) the stimulating electrode. A graph of the function $I(r)$ for responses of cells for which no fewer than 8 points were studied is shown in Fig. 2. Examples of direct responses of three neurons are given in Fig. 5: a, f, g. The latent periods of responses of different neurons varied from 0.2 to 0.3 msec and were independent of $r$. Stimulus duration likewise had no significant effect on the latent period although the thresholds rose appreciably if the duration of the stimulus was less than 0.1-0.2 msec (Fig. 1e).

The function $I(r)$ had one minimum, usually for $r$ between $-50$ and $+50 \mu$. In some cases, however, the threshold was minimal on removal of the stimulating electrode to 75-125 $\mu$ from the cell (Fig. 2). This could be connected with error in determining the location of the cell. For instance, with a neuron for which $I(r)$ reached a minimum at $r = 100 \mu$, the amplitude of the action potential was maximal when the recording electrode was displaced upward by 50 $\mu$ (Fig. 1b). The possibility cannot be ruled out that sometimes the low-threshold zone, stimulation of which led to the appearance of an action potential, did not coincide with the area of the neuron near which the most effective recording was obtained.

The neurons differed greatly in their response thresholds (Table 1). Response thresholds of cells located at a depth of 6.3-7.0 mm from the surface of the inferior colliculus ($H$ from $-0.3$ to $-1.0$) varied from 0.2 to 5.0 $\mu$A (below 1.2 $\mu$A in 10 of the 13 neurons). The response thresholds of neurons located more dorsally (at a depth of 5.0-6.2 mm) or more ventrally (7.1-8.5 mm from the surface of the