INTERACTION BETWEEN INTERZONAL AND AFFERENT IMPULSES IN THE SOMATOSENSORY CORTEX

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Extracellular recording of unit activity confirmed the existence of somatotopically organized connections between the two somatosensory areas of the cortex. Neurons of one somatosensory area, responding to peripheral stimulation, can interact only with cells of the other somatosensory area receiving impulses from homologous receptor zones. These experiments demonstrate that it is possible, in principle, for close interaction to take place between two areas of the somatic cortex in the course of sensory analysis.

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The existence of a second somatosensory area in the mammalian somatosensory cortex was established originally by Adrian [1] and confirmed later by Woolsey and co-workers [8-12]. After the discovery of a similar organization in the visual [6] and auditory [7] cortex, it became obvious that double representation of sensation is a general principle of the organization of sensory systems in the cortex. It can be supposed that the neurons of both somatosensory areas form the structural basis of a single, precisely functioning system of analysis of afferent impulses generated by stimuli of widely different types. Indirect evidence of this is given by the somatotopically organized interconnection between the two areas revealed by the method of evoked potentials [3-5], and also by recent morphological studies showing that interzonal connections in the somatosensory cortex terminate on dendrites of neurons in the deep layers of the cortex [2].

In the present investigation a combination of the method of evoked potentials and microelectrode techniques was used to analyze the connections between the two somatosensory areas and between interzonal and peripheral responses of cortical neurons.

EXPERIMENTAL METHOD

Acute experiments were performed on cats anesthetized with nembutal and on unanesthetized, immobilized animals on which operations were performed under local anesthesia. Evoked potentials were recorded from the surface of the cortex with silver electrodes. Single unit activity in one somatosensory zone located by the surface electrode was recorded extracellularly by means of glass microelectrodes filled with 3M KCl. Response potentials were evoked by direct stimulation of the zones of representation of the fore- and hind limbs in the other cortical area, and also by stimulation of cutaneous nerves of the contralateral forelimb (superficial radial nerve) or hind limb (sural nerve).

EXPERIMENTAL RESULTS

Points in the cortex receiving afferent projections from separate parts of the body in the first (CI) and the second (CII) somatosensory areas are joined by direct connections organized in accordance with the somatotopic principle characteristic of the representation of cutaneo-muscular sensation. For example, a response to stimulation of the representation of the hind limb in one zone was recorded only in the region of representation of the hind limb in the other zone and did not arise in the region of representation of the forelimb. This effect was seen especially clearly in animals anesthetized with nembutal. The existence of direct interzonal connections can be deduced not only from the latent period of evoked potentials from the cortical surface, but also from the ability of the neurons to undergo antidromic and direct orthodromic activation. Neurons located in the focus of maximal activity of the response region usually responded to stimulation of the other area with a high-frequency discharge consisting of 3 or 4 spikes. The discharges

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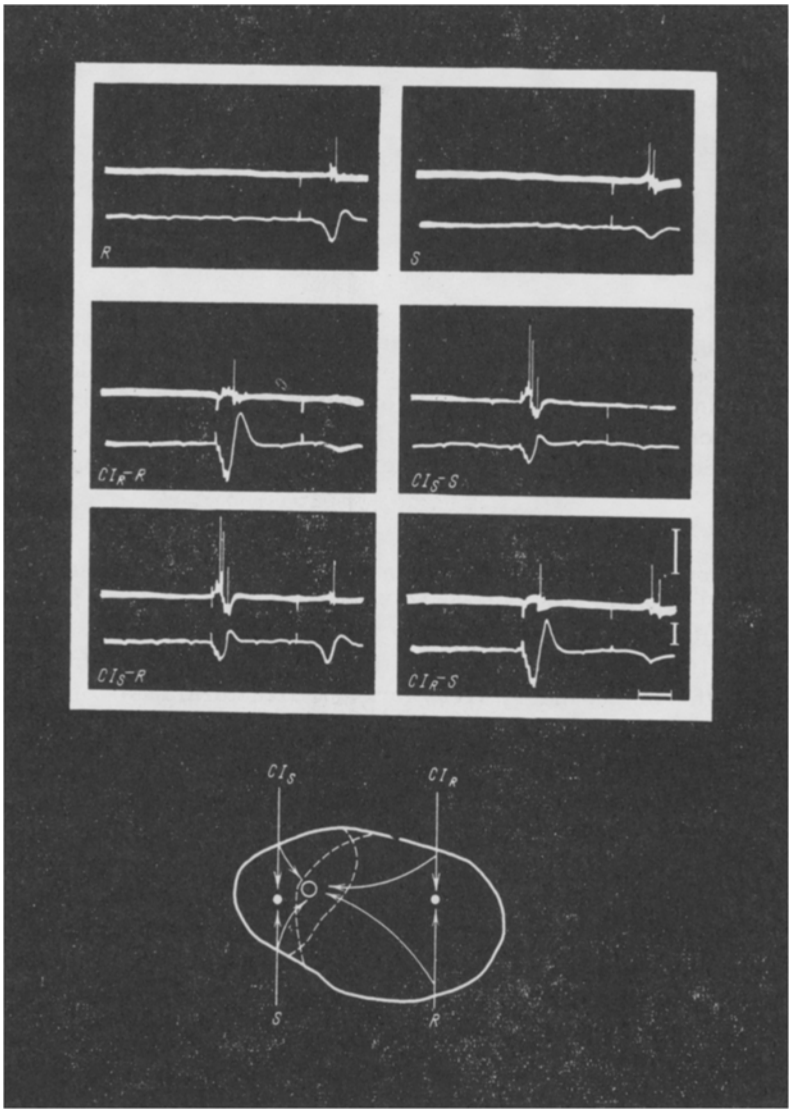

Fig. 1. Depression of potentials in the overlapping zone of afferent projections in cortical zone CII by preceding stimulation of the corresponding region in zone CI. Below: scheme explaining the experimental model. Zones of representation of the fore- and hind limbs in zone CII. Foci of maximal activity of sural (S) and radial (R) nerves indicated by dots; point of recording shown by a circle. Letters are explained in the text. Calibration of amplitude 0.5 mV, time 10 msec.

of these neurons coincided in time with the period of development of the initial positive and subsequent negative phases of the evoked potential of the cortical surface. As the microelectrode was moved from the focus of activity to the periphery of the region of representation, the amplitude of the surface response fell and short-latency discharges disappeared from the unit responses. In peripheral parts of the representation zone of that limb only the late discharges of the primary response, corresponding in time to the period of development of the surface-negative phase, remained. Similar changes in the cortical response were also observed in the case of movement, not of the recording electrodes, but of the stimulating electrode into the other area.

Preceding stimulation of the representation zone of the hind limb in one somatosensory area blocked the test responses in the other area to peripheral stimulation of the nerve of the same limb only, but did not affect the response of neurons in the representation zone of the forelimb.

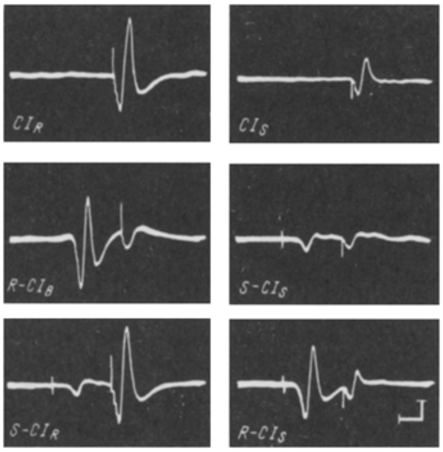

Fig. 2. Depression of interzonal potentials by preceding stimulation of the corresponding cutaneous nerve. Legend as in Fig. 1. Calibration of amplitude 0.5 mV, time 10 msec.

The principle of somatopic organization of connections of the two areas and of interaction between interzonal and peripheral responses could be clearly demonstrated not only in foci of maximal activity of the cortical representation zones, but also in areas of overlapping of afferent projections, to which excitation arrives from both the forelimb and the hind limb. In the experiment illustrated in Fig. 1, potentials were recorded in the overlapping zone of afferent projections of the sural (S) and radial (R) nerves closer to the focus of maximal activity in the representation zone of the hind limb. The localization of the electrodes could easily be judged from the character of the unit responses to peripheral and, in particular, to cortical stimuli applied alternately to the representation zones of the forelimb (CI_R) and hind limb (CI_S). Although responses from the surface of the cortex were of higher amplitude for the projection of the forelimb, the unit responses were more marked in the representation of the hind limb. This is explained by the fact that the amplitude of the combined responses in the projection zone of the forelimb during stimulation of the other area, just as that in response to peripheral stimulation, was always much greater than the amplitude of the responses in the hind limb zone. In other words, interzonal connections in the representation zone of the forelimb were much stronger than in that of the hind limb. Stimulation in the region of CI_S evoked a powerful short-latency volley of unit discharges at this point of zone CII, whereas stimulation in the region of CI_R evoked only a single discharge with a long latent period.

A preceding stimulus from the regions of CI_S or CI_R blocked only the corresponding peripheral response in CII and did not inhibit the responses of the same neuron to a peripheral stimulus from the other limb. Hence, only those neurons in zone CI which are activated by a peripheral stimulus from the corresponding limb affected the response of neurons in zone CII with an extensive receptive field.

In an experimental model of this kind the possibility of a block of the peripheral test volley, not immediately at the cortical neurons, but at the cells of the thalamic relay nucleus, sending somatotopically organized projections to both cortical zones, had naturally to be considered. Preceding cortical stimulation could excite the relay neurons of the posteroventral nucleus of the thalamus and, consequently, the system of reciprocal inhibition of these neurons, antidromically or through corticofugal connections.

To rule out the possibility of a blocking of the afferent volley at the level of the thalamic relay after preceding cortical stimulation of one zone, the same experimental model was used but the peripheral stimulus in this case was not the test stimulus, but the preceding stimulus (Fig. 2). In the case of this combination of stimuli, cortical responses in zone CII to stimulation of zone CI were blocked in the same manner although, as Sencer [5] previously showed, interzonal impulses are not transmitted through the thalamic relay, but conducted along intracortical connections. Finally, the possibility of a blocking of afferent impulses directly at the cortical level was not demonstrated by experiments in which responses from the cortical surface and action potentials of single units were evoked not by test stimuli from the nerve, but by direct stimulation of the relay nucleus itself.

These experiments demonstrate that close interaction between the two somatosensory zones in the course of sensory analysis is possible in principle.

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