CONVERGENCE OF IMPULSES ON NEURONS OF THE MOTOR CORTEX IN CATS ANESTHETIZED WITH CHLORALOSE

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Responses to electrodermal, photic, and acoustic stimuli recorded in neurons of the motor cortex of immobilized cats anesthetized with chloralose are little different from unit responses of cats immobilized with chloralose. This suggests that the occurence of responses to stimuli of different modalities, the similarity between them, and interaction of the blocking type under chloralose anesthesia cannot be explained by secondary effects associated with the motor response to the stimuli used.

Experiments with intracellular recording [3, 4] have previously shown that virtually all neurons of the cat's motor cortex from which recordings have been obtained under deep chloralose anesthesia give similar postsynaptic potentials (PSPs) to stimuli of different modalities. On the presentation of a second (testing) stimulus at an interval of between 20-30 and several hundreds of milliseconds after the first (conditioning) stimulus, in most cases no PSP appeared in response to the testing stimulus regardless of the modalities of the stimuli used (symmetrical interaction of blocking type). Under chloralose anesthesia relatively short-latency motor responses are often observed [1, 5, 6] to different peripheral stimuli. It has been suggested that the similarity between the PSPs and this type of interaction described above cannot be explained by the appearance (or blocking) of the motor response sending afferent impulses back to neurons of the motor cortex. At first glance this hypothesis would seem to be supported by comparison of the results obtained in experiments with extracellular recording of unit activity of the motor cortex in unimmobilized [2] and curarized [7, 8] cats anesthetized with chloralose. In the second case, the proportion of polysensory cells was appreciably lower than in the first.

A series of control experiments was accordingly carried out in which unit activity of the motor cortex was recorded extracellularly and intracellularly in cats anesthetized with chloralose and immobilized by injection of a relaxant.

EXPERIMENTAL METHOD

The methods of recording and stimulation (electrodermal stimulation of the contralateral forelimb and ipsilateral hind limb, flashes, clicks) were similar to those described previously [3]. In four of the seven experiments chloralose was injected (70 mg/kg intraperitoneally) initially, activity of some neurons was observed, and the relaxant (succinylcholine chloride) was then injected and artificial respiration applied. Ether anesthesia was used in 3 experiments. After the end of the operation the wound areas were anesthetized with xylocaine and succinylcholine chloride injected into the cat. After the activity of several neurons had been recorded in the unanesthetized animal, administration of chloralose began.

EXPERIMENTAL RESULTS

Activity of 40 cells was recorded in the animals under chloralose anesthesia. Extracellular recordings were obtained from 13 neurons, intracellular from 19, and quasiintracellular from 8. Of the 17 intracellular recordings, action potentials (APs) more than 40 mV in amplitude were observed in 9, while in the

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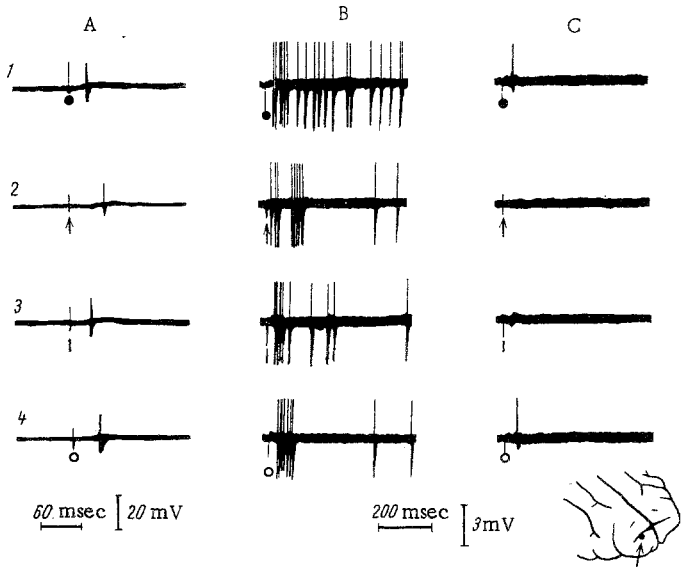

Fig. 1. Extracellular recording of responses of 3 neurons in the same experiment: 1) stimulation of forelimb (here and in Figs. 2 and 3, marked by a black circle); 2) photic (arrow); 3) acoustic (short straight line); 4) stimulation of hind limb (empty circle). Arrow on diagram points to site of recording; B) spikes extend beyond CRO screen.

rest, the mechanism of AP generation was inactivated by injury. Three neurons were recorded (and others were observed without being recorded) in animals under chloralose anesthesia before injection of the relaxant. The responses of these neurons were identical with those observed previously under similar conditions [3, 4]. In all experiments in which chloralose was administered initially, and in one of the three experiments in which chloralose was injected into a previously immobilized animal, similar results were obtained and they will be described together.

Extracellular Recording. Of the seven neurons recorded in these experiments six responded to all stimuli applied by a single spike (Fig. 1A) or a group of spikes (Fig. 1B), while one responded only to stimulation of the limbs (Fig. 1C). In this neuron, as in most of the others, spontaneous activity was virtually absent in the animals anesthetized with chloralose, and it was therefore impossible to decide whether an inhibitory response had arisen to flashes and clicks.

Intracellular and Quasiintracellular Recording. All 22 cells recorded responded to all stimuli used. The typical response (Fig. 2) consisted of a sequence of excitatory and inhibitory PSPs (EPSP and IPSP respectively). The EPSPs usually led to AP generation. In one cell an AP appeared only in response to photic stimulation. In another the threshold of AP generation was so high (about 22 mV; Fig. 3, A anc C) that nearly all EPSPs were subthreshold. No appreciable IPSP was observed in this case, probably because of the extremely high level of the membrane potential (the level was not measured accurately), close to the equilibrium potential for the IPSP. In this cell no significant spontaneous hyperpolarization waves likewise appeared (Fig. 3C). In neurons with a damaged spike generation mechanism, either the same responses were observed as in the other cells (i.e., EPSP–IPSP) or only the primary IPSP appeared. In one cell, after injury, there was a substantial decrease in amplitude of the IPSP, so that in response to all stimuli only depolarization (EPSP) began to be recorded.

Interaction between Stimuli. Interaction was investigated in four cells (two intracellular and two quasiintracellular recordings). In response to the simultaneous application of the two stimuli, or if a short interval (10-20 msec) separated them, sometimes a very small increase in the response was observed (Fig. $3A_3$) compared with the response to a single stimulus (Fig. $3A_1$), or this response was unchanged. If the intervals were longer, as a rule the test response did not appear regardless of the modality of the stimuli (Fig. 3A, B) until the interval reached the critical value of 200-400 msec. At intervals close to the critical

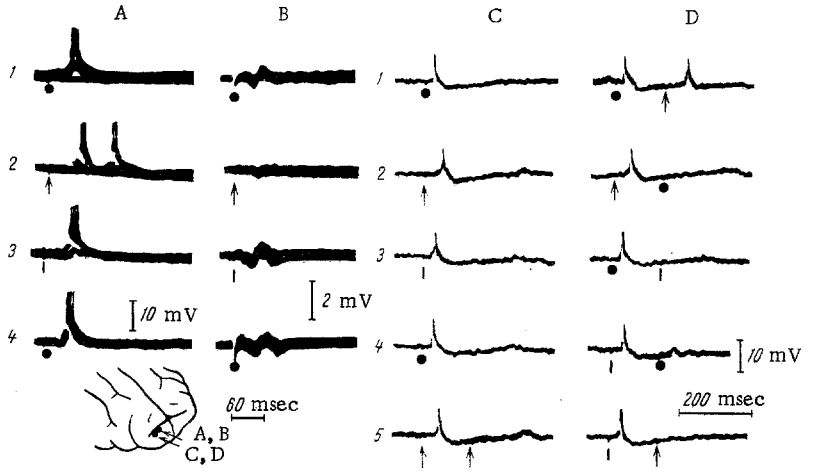

Fig. 2. Responses of two neurons to stimuli of different modalities. A) 1 neuron; B) record of focal potentials after death of this neuron; C, D) another neuron. In A-C: 1-4) the same stimuli as in Fig. 1. C_5 and D_{1-5}) application of paired stimuli separated by interval of 165 msec; two photic (C_5), electrodermal and photic (D_1, D_2), electrodermal and acoustic (D_3, D_4), and acoustic and photic (D_5). Electrodermal stimulation is conditioning for D_1 and D_5.

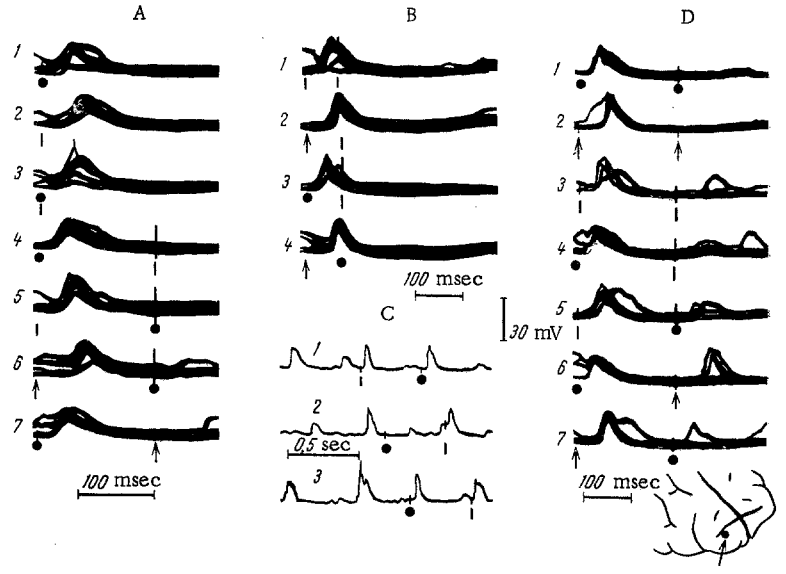

Fig. 3. Interaction between stimuli of different modalities on the same neuron. A: 1) stimulation of forelimb; 2) click; 3) simultaneous application of the same stimuli; 4-7) interaction of stimulation of forelimb with acoustic (4, 5) and photic (6, 7) stimulation with interval of 160 msec. Stimulation of limb is conditioning for 4 and 7; B) presentation of paired stimuli with interval of 80 msec: 1) two acoustic stimuli; 2) photic and acoustic; 3) electrodermal and acoustic; 4) photic and electrodermal; C) fragments of continuous record with paired stimuli. Interval between acoustic and electrodermal stimuli 430 msec; D) application of two stimuli of the same (1-3) and different (4-7) modalities with interval of 210 msec: 1) stimulation of limb; 2) photic; 3) click; 4-7) the same stimuli as in A_{4-7} respectively. In A_3 and B_3 one of the EPSPs evokes a spike of which only the lower part is shown.

value the testing responses either were weak (Fig. $3D_{4,5}$) or they did not arise in response to every stimulus (Fig. $3D_{6,7}$). Only in one cell did the character of the interaction depend strongly on stimulus modality; complete blocking of the response to photic stimulation did not occur after conditioning electrodermal stimulation (Fig. $2D_1$) nor was there a response to stimulation of the limb after a click (Fig. $2D_4$). If the same stimuli were applied in the reverse order, and also with all other combinations of stimuli, complete blocking of the test response was observed (Fig. $2C_5$, $D_{2,3,5}$). In all neurons investigated,the response also was frequently blocked to a stimulus applied a short time after a spontaneous PSP of suffiently high amplitude and with a suffiently steep ascending phase (Fig. $3C_2$).

In two experiments which were started on an immobilized, unanesthetized animal, administration of chloralose (90 mg/kg) did not lead to the appearance of responses typical of the other experiments. No well-marked focal evoked potentials, typical (see Fig. 2B) of animals under chloralose anesthesia, were observed likewise. In one of these experiments further injections of the anesthetic were given, increasing the total dose to 400 mg/kg, after which focal and unit responses were observed. However, even after this, responses to at least one of the stimuli were absent in three of the four neurons recorded. The reason for these phenomena is not yet clear. The suggestion is that the depth of anesthesia in these experiments was insufficient (because of individual differences between the animals or for other reasons). It is interesting to note that the total dose specified above in one of these experiments is three times higher than LD_{50} [6].

On the whole,the results of most of the experiments on immobilized cats demonstrated virtually the same pattern of convergence as was observed in the same experiments and had been thoroughly investigated previously [3, 4] on unimmobilized animals under chloralose anesthesia. The general pattern of the responses, their latent periods, and the character of interaction were very similar under these two conditions. This suggests that the appearance of motor responses is not the cause either of the completeness of convergence under chloralose anesthesia,or of the similarity of the responses to different stimuli, or of the symmetrical interaction of "blocking" type.

The relatively low proportion of polysensory neurons described in the literature [7, 8] can be explained partly by the use of extracellular recording, which does not reveal "subthreshold" convergence sufficiently clearly (Fig. 3). Another probable cause is differences in the experimental conditions and also, perhaps, in the dose of anesthetic, which is not specified by the authors cited.

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