

CHARACTERISTICS OF EVOKED POTENTIALS IN THE PARIETAL ASSOCIATIVE CORTEX OF THE CAT ANESTHETIZED WITH NEMBUTAL

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One of the most accurate methods of studying the morphological and functional organization of individual areas of the cerebral cortex is the method of evoked potentials (EP). Unlike the comparatively uniform primary responses (PR) of the projection areas, which have been described in detail, the EP in what are called the associative zones show certain particular features: they are very labile and their amplitude is small [13,17, etc]. During barbiturate anesthesia, these potentials disappear [2,17]. For that reason, the EP of the associative cortex is usually studied in unanesthetized animals or in animals anesthetized with chloralose.

Kruger and Albe-Fessard [18] directed attention to the negative attitude of many electrophysiologists to chloralose anesthesia, because it creates a state which is apparently incompatible with functional anesthesia of the brain. Considering that this conclusion was incorrect, like Buser and Borenstein [13,15,16], Fessard [17], O. G. Baklavadzhyan [4], and many others, they used chloralose to study the characteristics of the EP of the associative cortex. Fessard states directly that chloralose, which facilitates the conduction of impulses in the synapses, is suitable for analysis of associative EP; it synchronizes and strengthens the surface low-amplitude responses arising in these parts of the cortex. At the same time, this anesthetic complicates the analysis of the localization and properties of EP formation in the cortex, because it blocks certain inhibitory mechanisms [18]. Chloralose considerably modifies the pattern of the EP, enlarging and splitting the positive wave of the response, and most important of all, it leads to the appearance of EP over the whole surface of the cortex. Evidently, chloralose, facilitating as has been shown the conduction of impulses in the synapses, creates favorable conditions for conduction of afferent impulses along both the specific and the nonspecific systems [8]. For this reason, besides the excitation arising from a receptor stimulated experimentally, other types of ascending afferent impulses also enter the part of the cortex under investigation.

The object of the present investigation was to study the characteristics of the EP arising in the parietal associative cortex of the cat in response to stimulation of only two somatic nerves (sciatic and brachial). So far as possible, therefore, attempts were made to exclude all other forms of ascending afferent influences on the cortex, by using Nembutal instead of chloralose. By creating conditions for the conduction of impulses which differ from those created by the use of chloralose, Nembutal was a perfectly adequate type of anesthetic for these experiments. It blocks certain forms of activation from the subcortical formations, leaving unaffected only those pathways which conduct excitation from the periphery [1,3,5,8-10]. With the use of Nembutal, both phases of the response in the projection cortex were well defined, their amplitude was approximately uniform, and the EP were sufficiently reliable, showing stability and constancy of their pattern and latent period, and also some degree of localization.

EXPERIMENTAL METHOD

Acute experiments were carried out on cats. Monopolar recordings were made of the EP under Nembutal anesthesia of moderate depth (40 mg/kg body weight). The central end of the divided sciatic nerve and the nerve of the brachial plexus were stimulated.

EXPERIMENTAL RESULTS

In contrast to the results obtained by Fessard and co-workers [17], indicating the absence of EP during barbiturate anesthesia in the parietal associative cortex, clearly defined EP were recorded in the present experiments in this region (lateral and suprasylvian gyri).

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Comparison of Indices of Responses Obtained by Different Authors in the Parietal Associative Cortex during Stimulation of the Fore- and Hind Limbs of a Cat

Author	Type of anesthesia	Stimulation of forelimb			Stimulation of hind limb		
		Latent period (in msec)	Character of response		Latent period (in msec)	Character of response	
			Biphasic	Monophasic		Biphasic	Monophasic
Amassian	Chloralose	15-38	Present		15-38	+	
Buser and Borenstein [13]	Chloralose	15-40	"		Not studied		
Buser and Borenstein [14,15]	Chloralose	15-20	"		" "		
Thompson and co-workers	Chloralose	15-40	"		15-40	+	
Stimulation of ipsilateral nerve							
Fessard		15-20 and over	Present		Not studied		
O. G. Baklavadzhyan	Chloralose	Not studied			1) 20-40 2) Equal to latent period of negative phase of PR 3) Equal to latent period of PR		1) Typical positive 2) Atypical negative 3) Negative from projection cortex
Polyakova	Nembutal	6-8	Present as a rule	Negative in some cases	8-10		Negative

During stimulation of the sciatic nerve, EP were recorded in the associative cortex with a latent period equal to that for the PR in the corresponding somatosensory projection zone. Other authors have not observed such responses in the associative cortex, because according to their findings, the latent period of the associative EP was greatly increased by comparison with that of the PR (see table). In the present experiment, on the other hand, the pattern of the associative response differed from the PR: it consisted of one negative wave, frequently preceded by a very slight positive wave (Fig. 1). The amplitude of the response was small (mean 60-80 mV) and its duration was 10-12 msec.

These potentials were described as early associative responses (EAR), bearing in mind their short latent period, equal to the latent period of the PR in the focus of maximal activity (FMA) of the projection zone of the sciatic nerve (Fig. 1, 10).

Negative potentials, although differing slightly from those observed in these experiments, have been described only by O. G. Baklavadzhyan [4]. By using chloralose, in individual experiments he observed in the associative cortex monophasic negative potentials (in his terminology, primary associative responses), which he considered atypical for chloralose. The latent period of these waves was equal to the latent period of the negative phase of the PR of the projection cortex, i.e., it was slightly longer than the latent period of the EAR. In addition, small negative responses were found, repeated regularly before the associative positive response, with a latent period equal to the latent period of the PR. Baklavadzhyan, like Albe-Fessard and Rougel [12], suggests that this negativity is due to physical diffusion of the electrical activity arising in the projection cortex, for with the local application of KCl to this part of the cortex, this negative wave disappears. In the present experiment, the application of 2% and of a concentrated solution of KCl to the projection region had practically no effect on the EAR. The results of modification of these experiments shows that in their genesis, the associative EP in response to stimulation of the sciatic nerve and the nerve of the brachial plexus are independent of the PR arising in the projection zone of the cortex during stimulation of these somatic nerves.

It is important to distinguish the EAR obtained during this investigation from the negative responses observed by some other authors [6,11,19, and others]. According to these investigators, negative waves possessing the same latent period as the PR, or a slightly long latent period, were recorded either in the projection zone of the stimulated nerve or in the zone of representation of other modalities, but not in the associative cortex as in the present experiment.

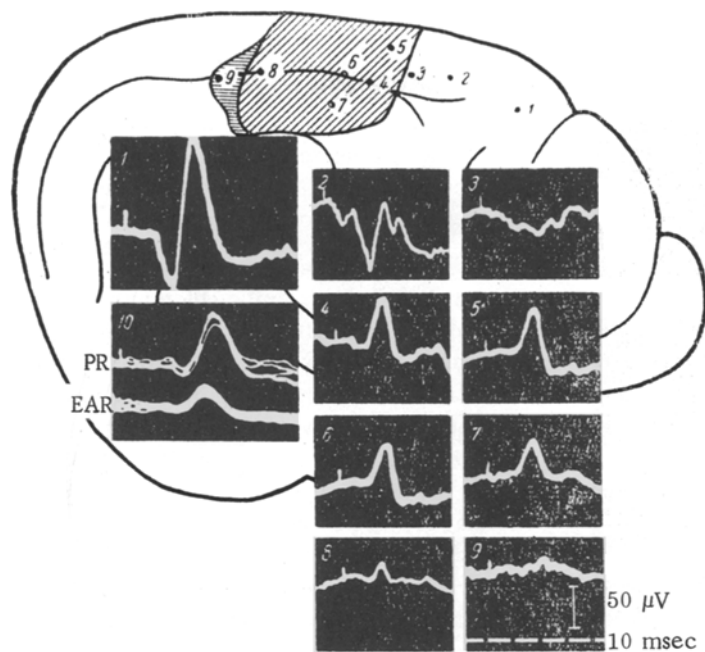


Fig. 1. Potentials evoked by stimulation of the sciatic nerve and regions from which they were recorded (shaded area) in the associative cortex (anteromedial, lateral, and suprasylvian gyri). 1) PR recorded in the focus of the zone of representation of somatosensory area 1; 2) PR recorded at the periphery of somatosensory area 1; 3) "zone of silence" between projection and associative areas of the cortex; 4-8) EP recorded at different points of the associative cortex: the zone from which EP indistinguishable from the general cortico-gram were recorded is shown by close shading (9); 10) comparison of latent period of the PR (top beam) and the EP of the associative cortex (EAR - bottom beam), equal to 10 msec.

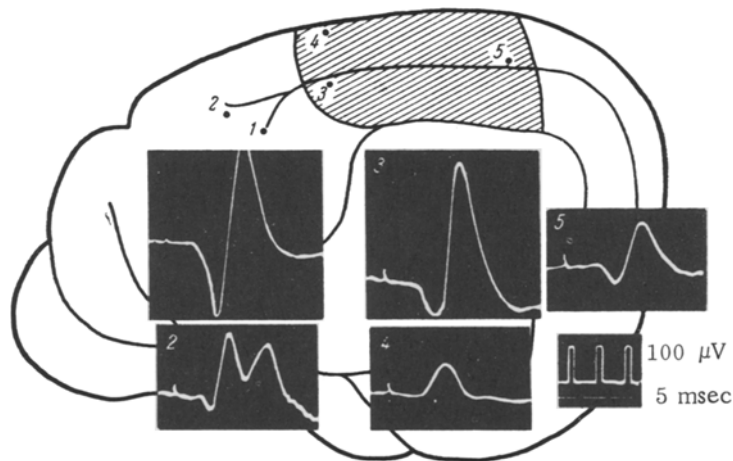


Fig. 2. Potentials evoked by stimulation of the nerves of the brachial plexus and region from which they were recorded (shaded area) in the associative cortex (lateral and suprasylvian gyri). 1) PR recorded from focus in the zone of representation in somatosensory area 1; 2) PR recorded at the periphery of somatosensory area 1; 3-5) EP recorded at different points of the associative cortex.

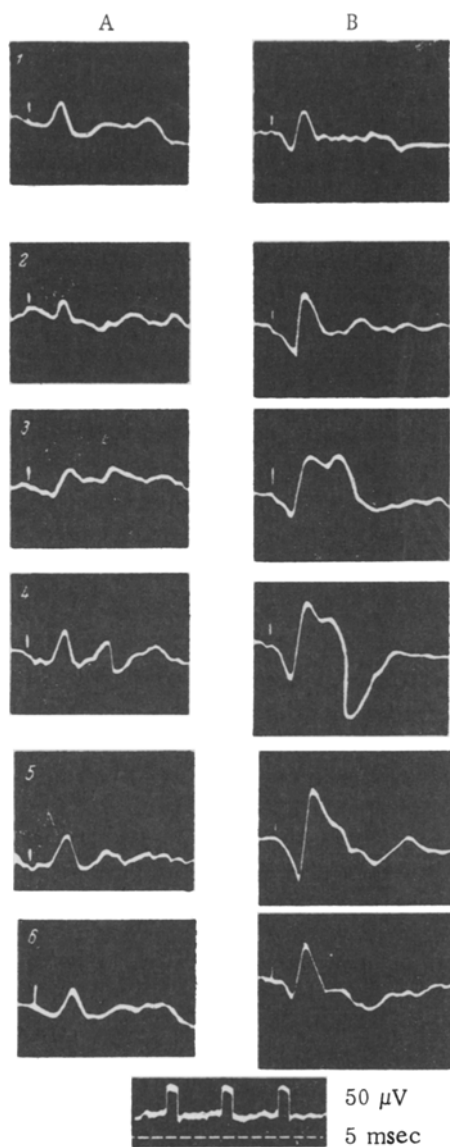


Fig. 3. Changes in the EP recorded at the same point of the associative cortex after local application of 1% strychnine solution to it. A) During stimulation of the sciatic nerve; B) during stimulation of the nerves of the brachial plexus. 1) Before application; 2-4) during application: for 1 min 30 sec (2), 3 min (3), and 5 min (4); 5) 1 min; and 6) 3 min after washing away strychnine.

of strychnine to the associative cortex, the response typical of Nembutal anesthesia was followed by the appearance of potential with a latent period of 20-25 msec of roughly the same type as during chloralose anesthesia (Fig. 3).

It was thus shown that during chloralose anesthesia, the EP of the associative cortex differ from the PR of the projection zones in their much longer latent period. They were therefore called nonprimary, or secondary. When Nembutal anesthesia was used, on the other hand, EAR were obtained which could not be described as secondary responses, because their latent period was the same as in the SMA of the projection cortex (8-10 msec). The

It is clear from Fig. 2 that, during stimulation of the brachial nerve, biphasic potentials appeared in the parietal associative cortex with a longer latent period than in the SMA of this projection region (6-7 msec in the anterior portion and 7-8 msec in the posterior portion of the associative zone). The latent period of the negative phase of these EP corresponded to the latent period of the EAR.

The responses described differed from the EP obtained by Fessard and co-workers, using chloralose anesthesia, in their shorter latent period (see table) and also in the shape and character of their distribution over the cortex. Buser [14] and Fessard [17] mention only biphasic responses; however, judging by the figures given in their article, a monophasic negative response could be recorded throughout the associative cortex. In the present experiment, negative waves regularly appeared only in the most orally and medially situated area of the lateral gyrus at its border with the sigmoid (see Fig. 2). In other parts of the associative cortex, the pattern of the response (biphasic positive-negative waves) was the same as in the projection cortex (see Fig. 2). Only in a few experiments was a purely monophasic negative potential observed here, although, as a rule, the negative wave of the EP was always enlarged by comparison with the positive. In addition, in the investigation conducted in Fessard's laboratory, the EP disappeared during barbiturate anesthesia; in the present experiment, they showed great constancy and stability, which incidentally is characteristic of the EP during stimulation not only of the forelimbs, but also of the hind limbs.

Analysis of the table shows that, during stimulation of both somatic systems in the conditions of chloralose anesthesia, biphasic or positive monophasic responses were typical. For Nembutal anesthesia, on the other hand, either negative potentials, sometimes preceded by a very small positive wave (stimulation of the hind limb), or a biphasic response in which the negative component was enlarged by comparison with the positive (stimulation of the forelimb) were characteristic. Hence, it may be supposed that the differences between the results of the present experiment, conducted under Nembutal anesthesia, and the investigations of other authors using chloralose anesthesia, can be explained by differences in the action of different anesthetics on the central nervous system. This suggestion is confirmed by Buser's findings [14]. Having compared the associative responses when using chloralose and Nembutal, Buser reports that during superficial barbiturate anesthesia, response was very irregular, while during deep anesthesia, it was replaced by secondary Forbes' discharges; during deep chloralose anesthesia, these potentials were concentrated and their amplitude was actually increased.

It may be concluded from the results of the present experiments that chloralose and Nembutal lead to the appearance of responses of different types, travelling along different thalamo-cortical systems. In this connection, the following fact observed in the present experiment is interesting. Following the local application of a 1% solution

associative EP during stimulation of the brachial nerve also possessed a relatively short latent period, much shorter than in the investigations of other authors, and the latent period of the negative phase, moreover, was equal to the latent period of the EAR. Accordingly, these responses also cannot be regarded as nonprimary.

The term "nonprimary," or secondary" responses in relation to the EP recorded in the associative cortex is, in the author's opinion, unfortunate. Most authors [4,14,17, and many others] do not differentiate between the secondary generalized responses spreading over the whole cortex and the local associative responses belonging to corresponding, clearly defined areas of the cortex. The two types of responses are related only by their similar latent period (in the present experiment even this resemblance is absent). K. M. Kullanda [6] attempted to classify the generalized and local responses of the EP. The present author also considers that a strict line must be drawn between the secondary generalized reaction and the associative responses. Responses recorded in the associative region should evidently be regarded as a special type of EP.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of the first issue of this year.