EVOKED POTENTIAL COMPONENTS IN THE LAYERS
OF THE AUDITORY CORTEX OF THE CAT

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Abstract. The intracortical distribution of evoked potentials was studied by seven-contact multielectrodes implanted into the primary auditory cortex of freely moving cats. The aim of the study was to compare the intracortical profiles of the responses evoked by click stimuli and by electrical stimulation of the medial geniculate body in different states of alertness and in Nembutal anesthesia. Only the early surface positive component showed phase reversal in the depth of the cortex. The middle latency components which were faithful indicators of vigilance appeared without phase reversal. Nembutal wiped out these components. A negative component of about 50 ms latency appeared in the attentive animal which had the highest amplitude close to the surface and decreased toward the depth indicating that it was generated in the most superficial layers of the cortex. The stimulation of the last nucleus of the specific auditory pathway elicited evoked potential patterns including also the middle latency components, which were closely similar to those induced by click stimuli.

INTRODUCTION

In the early periods of sensory neurophysiology, the evoked potentials (EPs) recorded from gross electrodes played an essential role in topographical mapping of sensory cortical areas (24). After a period of scepticism now the EP technique is in its age of renaissance. The study of
the event related potentials (ERPs) is widely used both in clinical neurophysiology and in experimental psychology (3, 14). In cognitive psychology ERPs serve as tools the use of which in complex experimental paradigms may help to reveal the consecutive stages of sensory information processing. One of the characteristics of this approach is the fact that physiological mechanisms responsible for these bioelectrical responses are not dealt with, because this problem is beyond the scope of cognitive psychology (22).

The interpretation of human ERP data, especially those related to the “endogenous” components is hindered by the fact that our knowledge about the source of these components is rather scanty (8). Information could not be obtained from the classical electrophysiological data, because these studies were carried out mainly in anesthetized animals in which the late EP components did not appear.

In spite of some recent valuable studies (1, 18, 19, 23), the gap between the analytical electrophysiological approach and the behavioral-psychological approach is still existing in research on sensory and perceptual processes.

Our experimental program was motivated by this problem. In an earlier series of experiments we found a correlation between the changes of the late components of the auditory cortical EPs in the cat and the animal’s general motive state (9). In different conditioning paradigms characteristic changes of certain EP components were also described (6, 10). These changes had some resemblance to those related to selective attention in human subjects (17). The study of the intracortical field potentials in the behaving animal seemed to offer an opportunity for the analysis of the origin of these evoked potential components. We developed a method which enabled us to record the evoked field potentials simultaneously in various depths of the cortex of the freely moving cat with chronically implanted multielectrodes (13). In the present paper we discuss the changes of the surface and intracortical EPs, elicited in different behavioral situations by clicks or electrical stimulation of the medial geniculate body (CGM).

METHODS

Eight adult cats were used in the present study. The electrodes were implanted under Nembutal anesthesia. The multielectrode, used for recording of intracortical field potentials, consisted of an array of six 75 μm diameter teflon coated platinum-iridium wires which were embedded in a small cylinder shaped acrylic block. (Fig. 1A) The wires protruding from the lower surface of the acrylic block entered the cortex
independently of each other lengthwise at an angle of 45 degrees. In their final position (Fig. 1B) the recording tips were located perpendicularly to the cortical surface, 300-400 μm below each other (for detailed description of the method see Karmos et al. (13)). In the present study the multielectrodes were implanted into the primary auditory cortical area (A.I.). To monitor the arousal level of the animal, conventional hippocampal and cortical recording electrodes were also implanted as well as electrodes for the recording of the electrooculogram and the electromyogram of the neck muscles. Bipolar stimulating electrodes made of enamel insulated 0.23 mm diameter stainless steel wires were implanted into the CGM. The inter-tip distance was 1 mm. All the electrodes and the socket were fixed to the skull with dental acrylic.

Clicks were generated at 3/s rate by 4 kHz sine wave bursts of 1 ms duration and were administered through a miniature bone conductor to maintain the acoustic input constant (12). For the electrical stimulation of the CGM 0.1 ms square wave pulses were used also with 3/s rate.

High impedance FET preamplifiers were used and the brain electrical activity was recorded on a Beckman Type 612 Dynograph and simultaneously on a Philips Analog 7 multichannel FM tape-recorder for further analysis.

The averaging of the EPs and the three-dimensional potential field figures were made by a TPA 1140 digital computer. Averaged responses were composed of 32 EPs.

RESULTS

The chronically implanted multielectrode enabled us to record the surface and intracortical auditory EPs in different behavioral states of the animal for weeks. The click stimuli were habituated before the beginning of the experiments. The clicks were given continuously during the whole recording session. Figure 1C shows the click elicited averaged EPs recorded from the surface (S) and from the consecutive depths of the cortex (2-6) in an alert animal. In Fig. 1D the first 50 ms epochs of each of these responses are presented as a computer generated three-dimensional potential field profile. The three-dimensional figure is formed by the cross-lines which connect the iso-latency points of the EPs recorded from the consecutive depths of the cortex. The peak latency of the first surface positive component was 11 ms. This early component displayed the so called "phase reversal" but the peak of the deep negative wave occurred 2 ms earlier than that of the surface positive one (Fig. 1D black arrow). This latency difference was characteristic only for the first component. The second negative wave following it did not
Fig. 1. The multielectrode and evoked field potentials recorded in the primary auditory cortex. A and B, Movement of multielectrode wires during implantation is indicated by an arrow (A), while the lower picture (B) shows the location of recording tips at their final position. C: Click evoked potentials recorded in the alert cat simultaneously from the surface (S) and from the consecutive depths (2-6) of the cortex. D, Computer generated three dimensional representation of the evoked potentials shown in C (for details see text).
show the phase reversal (open arrow). This wave appeared with highest amplitude in the middle layers and its amplitude decreased both toward the surface and toward the depth. Its latency was identical throughout the whole depth of the cortex.

The middle-latency phase of the response was characterized by a large amplitude positive-negative wave the form of which was highly dependent on the arousal level of the animal. This wave did not display the phase reversal either. The changes of the averaged EPs recorded from the surface of the A.I. area in the different stages of the wakefulness-sleep cycle are shown in Fig. 2A. In the highly alert animal, alarmed by an aversive signal, the late phase of the response was rather flat and a negative going component of 50-60 ms latency appeared (arrow). As the animal calmed down, the amplitude of this negative component decreased and the late positive-negative wave gradually developed. The amplitude and duration of this positive-negative wave complex were largest in the deep stage of the slow wave phase of sleep.

The intracortical profiles of the EPs in the waking and sleeping animal are displayed in Fig. 2B. These three-dimensional figures were generated by computer, so that the EPs recorded from the surface and from the consecutive depths of the cortex were drawn by thick lines and the spaces between them were filled in with additional curves calculated by linear interpolation. As the click stimuli were habituated and the acoustic input was kept constant, the early components displayed only minor changes in different behavioral situations. The intracortical patterns of the early waves were closely similar in the waking and sleeping animal. In the sleeping animal the later phase of the response was dominated by a large positive-negative wave, which appeared rather homogeneously throughout the whole depth of the cortex. The amplitude of the positive wave was largest in the middle layers of the cortex and decreased both toward the surface and toward the deepest electrode which was situated just at the border of the gray and white matter. In the waking animal this positive-negative wave decreased both in amplitude and in duration and the middle-latency phase of the response consisted of low amplitude waves. It can clearly be seen that the negative component appearing in the attentive animal (arrow) had its largest amplitude in the uppermost layer of the cortex and gradually decreased toward the depth. A similar intracortical distribution of the N50 wave can be seen in Fig. 1C.

In order to analyze the role of the specific thalamo-cortical input in the genesis of the behavior-dependent middle latency components, EPs elicited by electrical stimulation of the principal division of the CGM were recorded in different states of the animal. The EP patterns elicited
by click stimuli and by the CGM stimulation are compared in Fig. 3. The three-dimensional figures of the intracortical field potential profiles are shown in two different views for the better demonstration of the early and late parts of the responses. The overall patterns of the responses elicited by the CGM stimulation were closely similar to those evoked by click stimuli both in the alert and quiet animal as well as in the Nembutal anesthetized cat. Electrical impulses applied to the CGM induced a very sharp surface positive component in the A.I. area which had a "phase reversal", but the amplitude of the negative component in the depth did not increase as that elicited by click stimuli. The second negative wave following the earliest component had a similar distribution, but a higher amplitude. The middle-latency components were also similar and changed in identical way as those elicited by click stimuli, namely the positive-negative wave increased in amplitude and duration in the quiet animal while decreased in the alert state.

A considerable alteration in the pattern of the early components appeared when the animal was anesthetized with Nembutal (40 mg/kg i.p.). The peak latency of the click evoked surface positive component in-
Fig. 3. Comparison of intracortical patterns of evoked responses elicited by click stimuli (left) and by electrical impulses given to the medial geniculate body (CGM) (right) in the alert and quiet animal and under Nembutal anesthesia. The three dimensional potential field profiles are shown in two different views for better representation of early and late components.

Increased by 1 ms and the two early negative components in the depth of the cortex increased and merged into one large wave which invaded most of the cortex. This large deep negative component had two amplitude maxima in the medial and deepest layers. As a result the level of the phase reversal shifted toward the surface. The pattern of the response elicited by CGM stimulation was similar; the only difference was that the early deep negative wave had only one amplitude maximum in the middle layers.

The late phase of the surface EP recorded under deep Nembutal anesthesia was flat in spite of the fact that a large amplitude negative potential field could be detected by the intracortical electrodes. This late negative component was present only in the middle layers, as it did not appear in the surface record and decreased also in the deepest layers. This component of unexpectedly long latency (100-150 ms) was elicited by both types of stimuli.
DISCUSSION

Intracortical processes which are responsible for the generation of human ERPs can be analyzed only in electrophysiological experiments carried out on behaving animals. In the present study the intracortical distribution of the EP components was analyzed in the primary auditory cortex of the cat. The difficulty of this approach is that only few studies were carried out in which the correspondence was analyzed between the scalp recorded "endogenous" components and the components of the cortical EPs in animals (2, 4, 7). Further correlative animal studies are necessary in which paradigms similar to those used in human experiments are applied. In our study particular attention was paid to those "endogenous" waves which displayed characteristic changes in the behavioral experiments (6, 9, 10). However, a simultaneous recording of the surface and deep field potentials by the implanted multielectrode yielded some interesting data related also to the early "exogenous" components.

The peak latency difference between the first surface positive component and its deep negative counterpart, as well as the finding that the level of phase reversal changed its depth in different experimental conditions support the view that the simple dipole theory is inadequate even for the interpretation of the genesis of the early components (15, 16, 19). The fact that the second early negative component appeared without phase reversal questions the notion that the steepness of EP component is one of the preconditions of dipole reversal (5).

The middle-latency waves appeared with homogeneous polarity throughout the whole depth of the cortex. However, the maximum of the amplitude of these components appeared always within the cortical tissue which substantiated their intracortical origin. Of course more elaborated data processing techniques e.g. the current source density analysis (19) will be necessary for the more exact localization of the active generators.

That negative component which appeared in the activated, attentive animal had its highest amplitude in the most superficial layers and decreased in the depth without phase reversal. It is suggested that this component was generated by the synaptic action of the diffuse fibre network terminating in the superficial layers of the sensory neocortex (21).

The similarity of EP patterns elicited by click stimuli and by electrical impulses given to the last nucleus of the specific sensory pathway indicates that the time locked activation of the specific thalamic input is necessary and sufficient for the generation of the whole complex of cortical EP. In an earlier study we found that the lesioning of the prin-
principal division of the CGM abolished in the ipsilateral A. I. area all the components of the evoked response (11).

The changes of the middle-latency components of the CGM induced cortical EPs in relation to the animal's behavioral state question the direct role of a separate "nonspecific" cortical input in the genesis of these components. The reticulothalamic input either acts already through the CGM or, by continuously adjusting the functional state of the cortical neuronal network, it modifies the time course and the amplitude of EP components initiated by the specific sensory input. A more likely possibility is that the components following the early "exogenous" one are generated by multiple thalamo-cortical loops which are influenced by the diffuse subcortical input (20). The long latency negative potential field in the middle cortical layers of the Nembutal anesthetized animal supports this notion.

REFERENCES


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