A PRELIMINARY REPORT ON LOCALIZATION OF THE ACOUSTIC AREA IN THE CEREBRAL CORTEX OF THE DOG AS DETERMINED BY CLICK STIMULATION

by

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INTRODUCTION

The present work on the acoustic cortex was done preliminary to conducting experiments on the association system related to this projection area. This is a summary of the findings to date relative to the area responsive to click stimulation in the cerebral cortex of the dog. Although this area has been mapped in cats and monkeys and most recently in great detail by Woolsey and Walzl[1], in the cat, the extent of the area in the dog has never before been reported. The dog was chosen as an experimental animal for the reason that conditioning experiments being conducted by Doctor William F. Allen demanded further study (1) of the outline of the primary acoustic area in this species, and (2) of the association areas with which it is connected.

METHODS

Twelve dogs were used in this investigation. Nembutal was employed as the anesthetic agent in several of the early experiments, but a 10% urethane solution of Dial-Ciba* administered intra-peritoneally in doses varying from 0.4-0.65 cubic centimeters per kilogram, with subcutaneous supplementary injections during the course of the experiment, was used in most of the animals. An anesthetic level was maintained which abolished spontaneous movements and tendon reflexes, but the corneal reflexes were always present. Rectal temperature was observed and maintained at 37.5° C. by means of an electric heating pad under the animal. Following the insertion of a tracheal cannula, one cerebral hemisphere (usually the left) was exposed by retraction or

*The Dial-Ciba was kindly placed at the author's disposal by the Ciba Company.

removal of the temporal muscle, removing the cranium and zygomatic arch with rongeurs, and excising the overlying dura. The pial circulation was relied upon to maintain the moisture of the brain's surface, but occasionally warm Ringer's solution was applied. The margin of the wound was surrounded with cotton soaked in Ringer's solution to obviate muscle potentials. The ipsilateral ear was explored with the finger to assure patency of the external meatus and a suitable support was placed under the pinna if necessary. The animal's head lay tilted to the opposite side on the animal board. Lead electrodes consisted of two cotton wicks soaked in Ringer's solution. Monopolar leading was used throughout, the indifferent lead resting on the vertex of the intact side of the skull. The animal was grounded through the cotton padding. The leads from the animal passed through a 1.0 mfd. condenser to the input circuit of a five stage differentially balanced push-pull amplifier whose output was fed into a cathode-ray tube. The sound element consisted of an Allied type PC 1 relay with a 1/8 inch round brass arm 6 inches long soldered to the armature. The relay was mounted in a 4" x 4" x 2" metal cabinet of which one large face was open, and connected to the plate circuit of a 6F6 power amplifier tube, under usual conditions operating below the plate current cut-off point. Direct current impulses synchronized with the sweep circuit of the oscillograph were fed into the grid circuit of the above tube. Plate current would flow momentarily, causing the armature to pass through 0.5 centimeters at the contact points. Upon striking the lower contact, a click was produced, illustrated by a microphonic record in Figure 2-D. This click was the physiological stimulus. A microphone used simply to identify the time of arrival of the sound at the ear was set in front of the animal's head. The sound element was situated 30 cms. from the ear and the microphone. The output of the microphone was amplified, fed into a second cathode ray tube. The tubes were observed until a response was seen by exploring the brain with the active electrode. Simultaneous films were taken of the two tubes from twenty to thirty random electrode placements for each animal or until the responsive area was outlined. Higher gain and a faster sweep were used to illustrate the character of the response.

RESULTS

Reference to Figure 1 shows that the responsive area to the click sound, summarized from the data obtained on the 12 dogs, was predominantly limited to the dorsal end of the anterior ectosylvian and the cephalic portion of the middle ectosylvian convolutions; occasionally responses were obtained from the middle sylvian gyrus and from the ventral margin of the suprasylvian gyrus. Amplitude of responses was generally maximum at the center of this area with a progressive diminution as the margin was attained. Two distinct types of responses were found. One type occurred frequently but only in the anterior ectosylvian. It was characterised by a latency of 5-7 msecs. measured from the onset of the microphonic record, by an initial negative deflection of 25-50 microvolts, followed by relatively brief positive phase of comparable amplitude. From this positive peak a second type of sequence may or may not arise. This second type had an initial positive deflection succeeded by a longer negative deflection. This type is prominent near the center of the area where the positive phase possesses a spike character attaining an amplitude in some experiments of one millivolt, bearing a latent period of 8-11 msecs., followed by a large slow negative wave. Caudally along the middle ectosylvian gyrus the latency increases, temporal dispersion occurs, and the subsequent negative component becomes inconspicuous. Variation of the form of the responses occurred within the area. The most consistent characteristic of the responses was the presence of the initial positive deflection occurring from 8-11 msecs.

DISCUSSION

This investigation confirms the reports of Fischer(2), Kornmuller(3), Davis(4), Bremer(5), Bremer and Dow(6), and Ades(7) to the area of the cerebral cortex responsive to click stimulation in the cat. Kornmuller(3), Davis(4), Bremer(5), and experiments in this laboratory have yielded negative results for specific localization to stimulation with pure tones at different frequencies. Ades(8), Licklider(9), Woolsey and Walzl(1) by different methods have demonstrated tonal localization in the cerebral cortex of the cat and the monkey. Woolsey and Walzl(1) found that the area responsive to direct electrical stimulation of the cochlea includes the middle sylvian and ectosylvian gyri, the dorsal portions of the anterior and posterior ectosylvian gyri. There is a definite distribution of the cochlea within this area. This total area found by Woolsey and Walzl(1) compares with degeneration from the medial geniculate body demonstrated by Woollard and Harpman(10) and retrograde degeneration by Waller(11). Woolsey and Walzl(1) suggest that the narrow limits of the responsive area to click stimulation may be due to higher threshold of the neurones of the reminder of the system.

Although oscillographic studies as pointed out previously have not been made on the dog, other methods of investigation have been used. Ferrier[12] found that faradization of the transverse gyrus in the monkey resulted in pinna movements and a bilateral extirpation was followed by absolute deafness. From these results he concluded that the middle ectosylvian gyrus which upon stimulation results in similar movements in the dog was the acoustic end station for this species. Luciani and Tamburini[13] found that bilateral destruction of the middle and posterior parts of the "third external convolution" caused almost absolute deafness that was followed by some compensation. Munk[14] again working in dogs placed the auditory center entirely in the temporal lobe. Lesions here he observed to interfere with the animal's response to verbal commands. Luciani[15] shows the auditory center concentrated in the posterior border of the temporal lobe with an extensive radiation dorsad and cephalad to encompass almost half of the hemisphere. Larionow[16] attempted to demonstrate a "musical center" with tonal localization in the temporal lobe by means of ablation experiments. It is of interest that Pavlov[17] in his studies with the acoustic analyzer found that absolute deafness supervened only when the dorsal end of the anterior ectosylvian and the middle ectosylvian gyri were involved in the lesion, whereas bilateral temporal lobe lesions caused disturbances in the discrimination of ascending and descending scales of tones. It has been repeatedly shown by various experimental methods in primate material by Flechsig[18], Poliak[19], Walker[20], Le Gros Clark[21], Rundles and Papez[22], Ades and Felder[23], and by pathologic reports in human beings by many investigators that the transverse gyrus of Heschl is probably the acoustic projection in this species.

Initial positivity has been observed by Bartley, O'Leary, and Bishop[24], Woolsey, Marshall, and Bard[25], Woolsey and Walzl[1], and others as the response of a sensory cortex to peripheral stimulation under barbiturate anesthesia. It has been interpreted on the basis of drug action (Curtis[26]), microelectrode analysis (Bartley, et al[24]), and model experiments cited by various authors to be the sign of the impulse arriving in the axones of the afferent terminals which approach the surface from deeper structures. Initial negativity has been infrequently observed in responses of the cerebral cortex except in regions where the histological structure would suggest such a result (Hasama[27]). The origin of the late negative potential is speculative although studies in other parts of the cortex have yielded some facts toward their elucidation (Bartley, et al[24], Curtis[26], Adrian and Moruzzi[28], and others).

SUMMARY

The acoustic projection to this click sound has been located in the cerebral cortex of the dog and agrees in general with that found in the cat. It occupies an area extending over the dorsal extremity of the anterior ectosylvian gyrus and the middle ectosylvian gyrus, with minor radiations to the suprasylvian and sylvian gyri. Two types of responses are described: one, initially negative with a latency of 5-7 msecs. located in the anterior ectosylvian gyrus; two, an initially positive response of greater amplitude with a latency of 8-11 msecs.

centered in the middle ectosylvian gyrus.

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LEGEND

Figure 1: The responsive area to the click sound in the cerebral cortex of the dog. Summary of results from twelve animals. Each symbol represents responsive points for a particular dog. A, B, and C refer to points from which corresponding responses in Figure 2 were obtained.

Figure 2: A. Characteristic diphasic response from middle ectosylvian gyrus.

B. Response from anterior ectosylvian gyrus.

C. Monophasic response from posterior portion of middle ectosylvian. Records A-C at 60 cycles per second and 500 microvolts.

D. Microphonic record of the click sound.

E. Response from middle ectosylvian at 200 microvolts.

F. Anterior ectosylvian response at 100 microvolts. Records E and F at 200 cycles per second.

Upward deflection in all records indicates negativity of the active lead.

FIG. 1

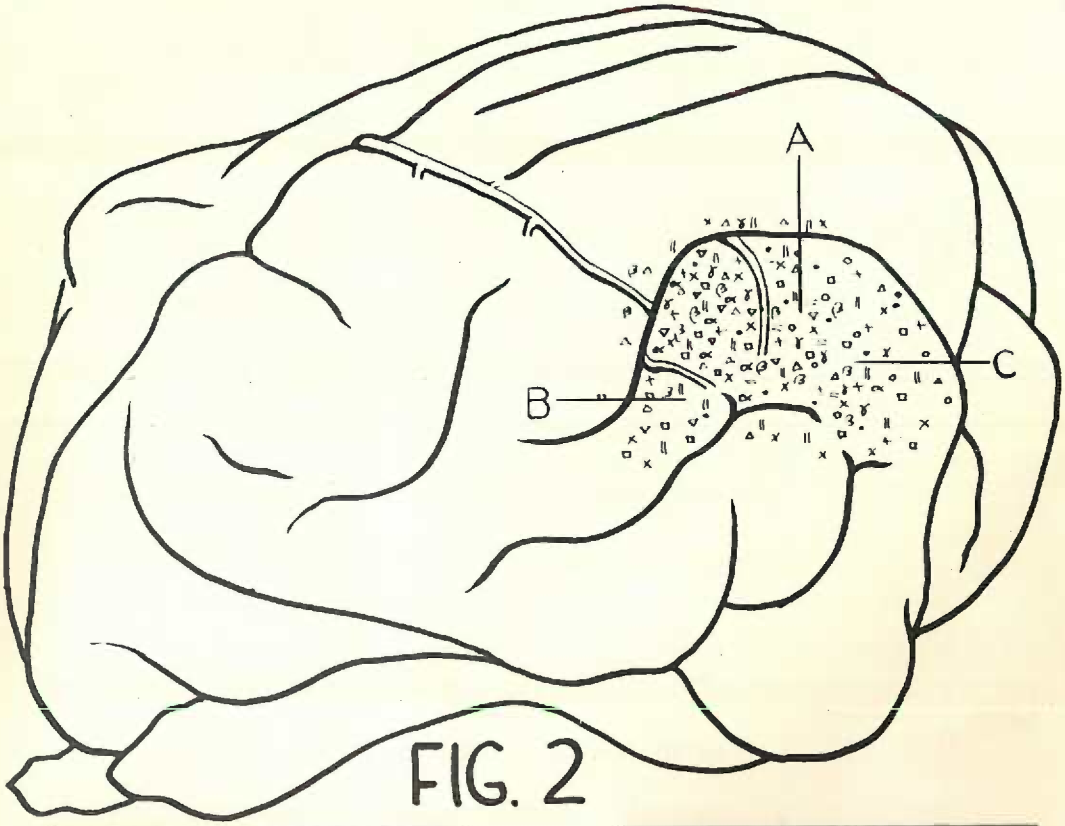

FIG. 2