STUDIES ON THE ACOUSTIC SYSTEM OF THE DOG

by

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A GENERAL INTRODUCTION TO THE ACOUSTIC SYSTEM

As a preface to this investigation, it is necessary to pursue a few of the initial efforts toward the localization of function in the central nervous system. Since Wernicke and Broca discovered their respective centers in the brain, much attention has been paid to the entire problem. The relation of the centers described by these two men to the sense of hearing have been adequately substantiated by subsequent studies as reviewed by von Monakow(1) and Pfeiffer(2) in human beings. In addition, Ferrier's(3,4) and Schaefer's(5,6,7) early studies on primates deprived of the first temporal convolutions have indicated the importance of the region to acoustic memory and recognition. These investigations, however, do not justify the conclusion that this is the region of incoming fibers to the cerebral cortex for the acoustic system. The anatomic demonstration of the radiations in primates and their origin in the medial geniculate body were dependent upon the investigations of Ferrier and Turner,(8) Minkowski,(9) Poljak,(10) Kornmuller,(11) Clark,(12) Rundles and Papez,(14) Ades and Felder,(15) Walzl and Woolsey,(18) Licklider and Kryter,(16) and Bailey, Bonin, Garol and McCulloch.(17) Their findings have led to the conclusion that the transverse gyrus of Heschl, occupying the superior surface of the first temporal gyrus is the predominant site of termination of the radiations. Poljak's study would further indicate a projection of undefined origin entering the angular gyrus.

Myelogenetic studies(19,20,21,22) in view of others' methods of approach assume some significance in localization of pathways. Flechsig and Vogt both found that the relationship of the medial geniculate body to the cerebral cortex is in the superior temporal gyrus. Cytoarchitectonic investigations (23,24,25) in part are found to agree with other methods. Brodmann's description of specific cellular structure of Heschl's gyrus, as an independent area, is justifiable. In the cat and dog, no such precise agreement is found between this method and other anatomic and physiological methods.

The primary large areas are readily distinguished. Recent oscillographic studies tend to discredit the division of the cortex into its areas of laminar cell structure.(26-37) The cortical potentials defy analysis on the basis of laminar structure.(38-54) Inasmuch as they are strictly electric field phenomena, another type of study of cerebral structure is essential(55-58) especially from the standpoint of units about afferent and efferent connections.(59)

The ear can physically be treated most satisfactorily as a receiver of sound energy. A receiver can be defined as a mechanism for detection of any of the characteristics of sound, viz., displacement, pressure, velocity, acceleration, etc.(60) The characteristic or group of characteristics which is actually detected by the ear is not known, although many hypotheses have been offered.(61) Certain facts are known about the cochlea and the mechanism of hearing. The frequency of the sound wave apparently can stimulate only a local region of the cochlea and the points of stimulation along the length are related in such a manner to the frequency that the distance is a logarithmic function of the frequency for the greater part of the range of hearing(62,78,36,37) or perhaps it may be related more closely to the so-called pitch intervals.(79) The amplitude of the sound wave is possibly related to the number of fibers stimulated and to the number of impulses along the individual fibers from a particular region of the cochlea.(77,78) Phase relationships are not detected by the ear.(80-83) This latter point is quite obvious in ordinary amplifiers where considerable phase distortion is present,(84) that can not be detected by the average ear. It is a problem to overcome in television receivers where it is necessary to reduce to a minimum any such distortion or to compensate for such distortion over a range of 20 to 3,000,000 cps.(85)

An impedance matching device exists in the mechanism of the middle ear, transforming the large displacement variations in air to those of large pressure variations in the medium of the inner ear.(60) The large differences between the specific acoustic resistances of air as compared to that of the bone and liquids of the tissues, a value which is of the order of several thousand, indicates that about 98% of the total energy is reflected in the absence of matched impedances.

The medullary nuclei upon which the cochlear nerve projects has been known for a long time, but the relation of individual parts of the cochlea to these nuclei is of recent origin.(86) The course of the acoustic system through the medulla to the mesencephalon and diencephalon is generally agreed upon(87-103) but in its finer aspects much discrepancy exists. No localization has been shown for fibers along this path. A point of dispute has been the course of the ipsilateral fibers to the cerebral cortex, centering chiefly around whether the fibers attain their course at lower levels, which seems to be the case in cats and dogs,(104-106) or at higher levels, such as in the region of the inferior colliculi.(107) Crossing is denied in the primates in physiological experiments on the pathways.(18) In addition there is apparently a species difference between the rabbit and the cats.(106)

Localization has been demonstrated in the medial geniculate body for different frequencies.(108-109) This bears confirmation by other methods.

The early investigations employing oscillographic means of recording used sudden clicks for stimuli. By this method Fischer,(110) Kornmuller,(11) Davis,(111) Gerard, Marshall and Saul,(112) Hawkins, J.E., Jr.,(115) Bremer,(113) Bremer and Dow,(114) and Ades(116,117) have outlined the area responsive to clicks in the cortex of cats and dogs. Walzl and Woolsey(118) have shown that responses to clicks are lost in certain regions of the acoustic cortex by cochlear lesions.

That stimulation of the local regions of the cochlea can excite specific regions of the cerebral cortex, both by electrical stimulation and by the use of pure tones is established.(36,37)

There is also apparently a rather complex arrangement of this projection arising in the medial geniculate body. These physiological experiments are supported by recent studies on the anatomical connections of the medial geniculate body to the cerebral cortex in the cat.(119,120) In the cat and dog the area of the cortex involved occupies the middle ectosylvian gyrus as well as the dorsal portions of the anterior and posterior ectosylvian gyri and the sylvian gyrus.(36,37)

Unpublished experiments by Allen on dogs deprived of the above area, indicate other afferent fibers can be used for correct conditioned differential foreleg responses. A new area receptive to impulses from the cochlea has been found,(121) that is not directly related anatomically to the other areas. Recent studies on this area suggest that it is significant.

Audio Frequency Localization in the Acoustic Cortex of the Dog

The areas of the cerebral cortex to which the acoustic system projects have not been reported in detail in the dog, although Ferrier(3) pointed out many years ago that the middle ectosylvian gyrus of this animal is the cortical zone for hearing. Woolsey and Walzl(36) recently have shown that the cochlea is represented in the cerebral cortex of the cat, by electrical stimulation of the bony spiral. Preliminary reports of audio frequency localization in various species also have appeared in recent literature. Studies now in progress on the acoustic association connections of the dog made necessary a more exact investigation of the areas receptive to tones in this species. Experiments to this end, both by audio and electrical stimulation, were therefore undertaken, the results of which are presented in the following pages.

Methods. The animals were deeply anaesthetized with nembutal or with a 10% urethane solution of Dial-Ciba. Usual surgical supportive measures maintained the condition of the animal. The ectosylvian and sylvian gyri were exposed with a circular cranial opening, which was liberally surrounded with cotton soaked in Ringer's solution. A shett lead ring 9 cm. outside diameter and 6 cm. inside diameter was embedded in the cotton, concentric to the opening. The ring was grounded and through a cotton bridge soaked in Ringer's solution, served as the indifferent electrode.(57) The active electrode was a cotton wick moistened with Ringer's solution which was moved over the cortex in 1 to 2 mm. coordinate divisions. The indifferent and active electrodes were led through 1.0 mfd. condensers to the input of a 5 stage differentially balanced push-pull amplifier whose output was fed into a cathode ray tube.

Acoustic stimulation: The audio frequency signal was generated by an oscillator,(122) whose output was fed in another room into the grids of a 79 tube.(123)

Direct current impulses synchronized with the sweep circuit of the oscillograph were fed into the grid circuit of a 6F6 power amplifier tube, operating below the plate current cutoff point. The flow of plate current in the 6F6 tube, caused by these pulses, activated a relay which eliminated a high negative grid bias voltage in the 79 tube, allowing the audio signal to flow into a baffled loudspeaker. An attenuator was placed in the input circuit of the 79 tube to reduce the minimum output of the oscillator. The output of the oscillator was considered constant over the range of 100 to 8000 cps.

For uni-lateral stimulation, after destruction of the cochlea of the opposite ear, a loudspeaker was placed directly opposite the animal's ear at a distance of about 1 meter for the contra-lateral and 1/2 meter for the ipsi-lateral side. The initial click free wave front from the loudspeaker constituted the physiological stimulus. Because of non-uniformity of any loudspeaker response,(124) modification of sound by conduction, and lack of suitable microphonic equipment, no calibrations were made in terms of decibels. In conformity with neurophysiological methods, the stimulus value is denoted as threshold, maximal, sub-maximal and supra-maximal for the cortical response. The cortical focus of a frequency was determined by using a minimum threshold stimulus.

A microphone situated at the level of the oval window was connected through another amplifier into a second cathode ray tube.

Electrical stimulation. After exposure of the cochlea, stimulating electrodes, consisting of the tips of a pair of No. 40 enamel covered copper wires, were placed on the bony lamina 0.5 to 0.7 mm. apart. The shock was a condenser discharge of a magnitude causing a threshold cortical response.

Twelve dogs were used in the present study; 3 for ipsi-lateral, 3 for contra-lateral, and 1 for both contra- and ipsi-lateral audio frequency stimulation; 4 for ipsi-lateral and 1 for contra-lateral electrical stimulation of the cochlea.

Results. Responses from the contra-lateral cortex possessed a lower threshold than those of the ipsi-lateral side. On both sides the usual initial response for the focus of a frequency was surface positive (Fig. 5). With supramaximal stimulus values, small surface positive responses were recorded for a distance of several millimeters from the suprasylvian and the dorsal portion of the coronal gyri. Initial negativity was encountered in all experiments in various parts of the cortex, but was consistently present along the middle and anterior ectosylvian gyri bordering upon the suprasylvian sulcus (Fig. 3). The negativity was obtained to all audiofrequencies, to the electrical shock, and has been observed to click stimulation. One point was responsive to a wide range of frequencies.

Contra-lateral side. Figure 2 illustrates the foci of response for various frequencies of the dorsal area (Fig. 1) along the middle ectosylvian gyrus, high frequencies anteriorly and low frequencies posteriorly. Thresholds varied with frequency---decreasing toward the high. The outlines represent the responsive area for each frequency studied at its own threshold value. In general, responses were largest near the centers of the foci, with diminishing size and variation of latencies as the periphery was approached. The foci were arranged linearly about 2 mm. apart, with neighboring frequencies related to each other as octaves. Responses to 20,000 cycles, the maximum output of the oscillator, were found anterior to and overlapping considerably with the area for 16,000. A moderate concentration of foci was observed for frequencies 100 to 400.

Ventrally, on the anterior ectosylvian gyrus, responses which required a stimulus supra-maximal for the dorsal area were obtained to frequencies 100 to 800, but, with smaller intervals. Frequencies 4000 to 16,000 elicited responses from the poster ectosylvian gyrus with a similar pattern. Those of 800 and

4000 appeared to spread toward the ectosylvian sulcus. Responses to 1600 and 2000 were recorded from these areas into the region of the sulcus and the sylvian gyrus. Discrete foci from the sylvian gyrus were obtained infrequently. Under deep anesthesia (Fig. 2) responses to 4000 were limited to the posterior, ectosylvian gyrus, and responses to 800 to the anterior ectosylvian gyrus, spreading slightly upon the sylvian gyrus. Localized points of response to 1600 & 2000 were found upon the sylvian and posterior ectosylvian gyri. Under lighter anesthesia, the areas for 400 and 800 spread upon the anterior portion of the sylvian gyrus, 4000 spread from the posterior ectosylvian gyrus over the sylvian gyrus, while 1600 & 2000 extended from the margins of the area responsive to 16,000 across the sylvian gyrus to include a large portion of the area for 800. The responses to 800, 1600, 2000 and 4000 upon the sylvian gyrus were small, 50-100 microvolts. In the latter experiment the sylvian gyrus was removed along the ectosylvian sulcus and the adjacent walls of the ectosylvian gyrus were explored. Responses were obtained anteriorly to 400, 800, 1600 and 2000; behind and dorsally to 800, 2000 and 4000. Frequencies of this ventral area were arranged in an inverse order to those of the dorsal area.

Ipsi-lateral side. The distribution of the responsive foci for the ipsi-lateral side resembles the contra-lateral side in detail.

Electrical stimulation. (Fig. 4). Stimulation of the ventral curve of the base of the cochlea with a condenser discharge at threshold strength gave a responsive area in the anterior end of the middle ectosylvian gyrus. With supra-maximal stimulus, an area was outlined upon the posterior ectosylvian gyrus. Stimulation of the middle coil produced a responsive area in the mid portion of the middle ectosylvian gyrus, with or without its area of high threshold on the anterior portion of the sylvian gyrus. The ventral area on the sylvian gyrus, when demonstrated at identical stimulus values to those of the apex and base, occupied only a few square millimeters, with small responses. Stimulation of the apex activated a region on the posterior extremity of the middle ectosylvian gyrus and with stronger stimulation a focus upon the anterior ectosylvian gyrus. The dorsal and ventral areas were bilaterally represented with greater activation on the contra-lateral cortex for equal stimulus values.

Discussion. Ferrier(3) and Luciani and Tamburini(125) early concluded that the middle ectosylvian gyrus in the dog was an important landmark of the acoustic system, although Luciani(126) later found the cortical acoustic area to be more extensive. Munk(127) and Larionov(128) emphasized the temporal lobe as an "auditory sphere." Their physiological experiments, however, do not distinguish between the interruption of discrimination and that of association. The present investigation substantiates Luciani's(129) physiological demonstration for the existance of an "uncrossed" pathway to the cerebral cortex of the dog. Babkin(69) in Pavlov's laboratory found that absolute deafness supervened only when the anterior ectosylvian and middle ectosylvian gyri were included in their temporal lobe lesions. Pavlov attributed the loss to subcortical structures. Temporal lobe lesions involving the posterior portion of the area outlined in the present investigation disturbed transiently conditioned alimentary reflexes to individual tones, but seriously impaired discrimination of ascending and descending tonal scales. The experiment of Eliason, described in Pavlov's book, deserves mention. A reflex was established to a chord, 85-256-768 dv. Each component produced a reaction less than the entire chord but equal among themselves. The lesions, including the acoustic area of the present demonstration with the exception of the anterior portion of the anterior ectosylvian gyrus, resulted in loss of response to 768, but increased reaction to 85 and 256. 768 with reenforcement reassumed its conditioning properties.

The lesion removed the greater portion of the ventral area responsive to 800, leaving intact areas for 100, 200 and 400.

Results of audio frequency stimulation are supported by electrical stimulation of local regions of the cochlea. Both phases of the present investigation show in the dog that the extent of cortical localization and its divisions into two areas differing in location, threshold, and pattern is similar to the condition described in the cat by Woolsey and Walzl (36) by the electrical method. For their "primary" and "secondary" areas, dorsal and ventral, respectively, have been substituted to avoid implication of knowledge of the functions of such areas. Audio frequency stimulation adds information concerning localization which is unobtainable to electrical stimulation. As at the cochlear level,(68) the arrangement of successive octaves at equal intervals is apparent in the dorsal area of the cerebral cortex. This was shown by Woolsey and Walzl(36) for the basal turn of the cochlea. The moderate concentration for 100 to 400 may be due to harmonic distortion since strong stimulus values were used. However, separation of foci indicates the activity of the fundamental. If the distance between two foci of excitation (or inhibition) in the cortex is necessary for the discrimination of two tonal stimuli, this suggests an explanation why the intervals of the chord, thirds, fifths, eighths, etc. of the harmonic scale are recognized as equal or identical irrespective of pitch level.

The ventral area does not exhibit the same relation of interval to distance, but concentration of foci of the high and low frequencies with dispersal of the intermediate frequencies. However, within the areas of concentration, slight shifts of foci are evident. Such a pattern may be merely apparent because irradiation with intense stimuli, possible at several levels, namely, cochlear,(78) geniculate(36) and cortical,(43) could account for less discrete localization. Or, it may be real, for the development of the middle ectosylvian sulcus in the dog, together with the demonstration of responses within the sulcus, and the diminutive character of responses from the sylvian gyrus would indicate lengthening and dispersal of the cortical area for the intermediate frequencies, as well as reduction in the number of fibers to the sylvian gyrus. The responsive area in the present work agrees well with Campbell's(24) histological type for ectosylvian B cortex, but disagrees with the statement that the ectosylvian A cortex is the main projection area. His classification is supported by neuro-physiological investigations in other systems.(130,131,26)

Retrograde studies(120) and Wallerian degeneration(119) on connections of the medial geniculate body with the cortex in the cat support the oscillographic studies of Woolsey and Walzl.(36)

Consideration of the electrical sign of cortical afferents and latency measurements must be postponed until further data are available.

Further Afferent Fibers to the Acoustic Cortex of the Dog

The purpose of this study is to explore the cerebral cortex for the presence of other areas for reception of sound impulses, other than those reported previously.(37) This was suggested by some unpublished findings by Allen in which the auditory cortex of the dorsal and ventral areas was extirpated or coagulated thermally and the dog was able ultimately to re-acquire correct conditioned differential responses with the foreleg to bell and iron cup stimuli.

Methods. Dial-Ciba and pentobarbital sodium were employed as the anesthetic agents on alternate experiments. In general the technique of tonal and electrical stimulation and the method of recording have been described in the previous investigation.(37) The following alterations to the details of the technique were made. For tonal stimulation the loudspeaker was placed about 30 cms. from the animal's ear and the tones were presented at full gain of the amplifier. The wave front of tones ranging from 100 to 16,000 cps. at intervals of frequency bearing the ratio of 2/1 were employed and this portion of the cortex was explored for responses in one mm. coordinate divisions.

In electrical stimulation, condenser discharges were led through copper wires to produce an electric field on the apical, middle, and basal turns of the bony spiral. The responsive foci in the dorsal and ventral areas of the cortex were outlined to stimulation of these three points of the cochlea at their threshold values to assure that the electrodes were situated at optimum positions.

With electrodes on either the middle or apical turn of the dissected bony spiral, the modiolus was effectively severed by means of a dental chisel introduced between the basal turn and the bony orbit of the cochlea.

Intracranial section of the eighth nerve was accomplished through an opening in the occipital bone following exposure of the nerve by gentle elevation of the cerebellar hemisphere with a small retractor.

The dorsal and ventral areas were either removed to a depth of one cm. with a spatula, or coagulated by means of a hot knife.

Twelve dogs were used in this investigation.

Results. The responsive area in the cerebral cortex to tonal stimulation of the intact cochlea and to electrical stimulation of the bony spiral of the dissected cochlea is illustrated in Figures 6 and 8, respectively. It occupies about 9- 20 sq. mm. of the cortical surface on the ventral extremity of the anterior ectosylvian gyrus where the latter unites with the coronal gyrus to form the anterior composite gyrus. In several experiments, responses were obtained from a portion of the cortex extending 1-2 mm. upon the posterior margin of the adjacent coronal gyrus. This location of the responsive area was quite constant from one animal to another. In most instances, it was isolated from the ventral area by an unresponsive region, although an occasional small initially negative response was found in the dorsal portion of the intervening strip of cortex.

Responses from the surface of the cortex were obtained bilaterally with electrical stimulation of the bony spiral (Figs. 9 and 10), but only on the contra-lateral side with stimulation by means of the tones. This may be due to the low output of the amplifier. Responses to electrical stimulation of the ipsilateral side were small (Fig. 10) even with strong shocks. There appeared to be some indication of localization but the overlap, particularly in so small an area, was of such magnitude that the point cannot be stated with certainty.

To electrical stimulation of the apical, middle and basal turns, the amplitude and distribution of the cortical responses were about equal (Fig. 9). The threshold was surprisingly low but was higher than for the dorsal or ventral areas. Tones giving cortical responses were 800, 1600, 2000, 4000, 8000 and 16,000 cps. (Fig. 7). Occasionally 400 cps. gave a response, but responses to 100 and 200 cps. were not found in these experiments. These two frequencies had to be given at full gain of the amplifier to obtain responses in the dorsal and ventral areas. The responses to both tonal and electrical stimulation were characteristically surface positive and possessed latencies (7-10 msecs.) comparable to those of the dorsal and ventral areas (Figs. 7, 9 and 10). The amplitudes graded off at the periphery of the area and reached maximums within the area of 200 to 500 microvolts.

With an intensity of the electric field above the threshold for thisarea, application of the stimulus through the copper wires to the mucous membrane of the middle ear, particularly over the cochlea, did not evoke any responses in this region of the cortex. Abolition of responses to electrical stimulation of the middle and apical turns of the bony spiral was shown to follow severance of the modiolus below the basal turn (Fig. 11). Shocks applied through electrodes placed on the severed stump were still effective in causing the responses.

The magnitude of the cortical responses to the sound wave were diminished but not abolished by placing a solid obstacle between the loudspeaker and the animal's ear. Extirpation or coagulation of the dorsal and ventral areas (Fig. 6) to a depth of one cm. did not prevent the responses.

Intra-cranial section of the eighth nerve abolished the cortical responses to the tones (Fig. 12). Examination of the brains revealed that the 8th nerve was completely severed lateral to its entrance into the medulla without injury to the 7th nerve or the medulla.

DISCUSSION

Von Monakow(1) destroyed the ventral parts of the posterior sylvian, ectosylvian, ectolateral and composite gyrus in a cat which resulted in almost complete degeneration of the medial geniculate body. An illustration of a transverse section of the specimen shows a gross enlargement of the ventricle and thinning of the white matter of the entire hemisphere. The destructive process in the cerebral cortex appears much greater than the extent of the lesion.

In Dog S of Luciani's experiments(132) the successive multiple extirpations of the posterior halves of the cerebral hemispheres included the area described in this paper. These lesions markedly disturbed the reactions of the animal to the hearing tests. The hearing tests, consisting of turning the head, flicking the ear, to a tuning fork, to noises, to the sound of dropped food, were simple and could represent subcortical reflexes. However, Luciani concluded from his experiments that the animal was deaf as a result of the lesions. The other significant extirpations by Luciani were complicated by the presence of meningitis and abscesses and can in no way justify the conclusion that the auditory area is as extensive as he described.(126) The investigations by Munk,(127) Alt and Biedl,(133) Kalischer,(134) Rothmann,(135) Swift,(136) and Pavlov(69) do not include this area.

The proximity of the area to the tactile system has received particular attention, because of the possibility that tactile endings were stimulated by the sound wave or by the electric field. Marshall, Woolsey, and Bard(35) have obtained responses in this region to bilateral tactile stimulation of the forepaws in the cat. General cutaneous representation of both fore and hind paw was found by Adrian(130) in the cat and dog but only to contra-lateral stimulation. Representation of the 5th nerve was found by the latter investigator upon the coronal gyrus. The present findings indicate that responses are also obtained in this region from the cochlea or its environment. Certainly the 5th nerve and the mucous membrane of the middle ear is excluded as the source of the potentials. Since the seventh nerve in its course through the temporal bone passes near the cochlea and innervates structures of the middle ear, it must be considered as a possible source of the potentials. If the electric shock is too strong, movement of the facial muscles is elicited. However the cortical response is abolished by severing the modiolus at its base.

By employing tonal stimulation careful intra-cranial section of the 8th nerve alone without injury to the 7th makes it apparent that the impulses come from the 8th nerve and probably from its cochlear division, since section of the modiolus abolishes the potentials to the electric shocks applied to the bony spiral.

Since extirpation results indicate that this area is not related to the dorsal and ventral areas, it is concluded that the responses probably arise in subcortical centers by irradiation.

The ventral extremity of the anterior ectosylvian gyrus lies in a region from which Bechterew and Mislawski(137) and others by faradic stimulation obtained salivary secretion mediated by the chorda tympani. Mann(31) discovered in the cat a walking type of movement of the front leg at one point and a hind leg movement at an adjacent point by stimulating this region of the cortex with a faradic current. By placing one electrode over each point he was able to elicit a peculiar walking or more nearly a swimming motion. Garol(33) has confirmed the excitability of this part of the cortex, finding similar running movements and an arrangement of the body pattern in an inverse order to that of the generally accepted excitable cortex.

SUMMARY

The general aspects of the acoustic system were briefly summarized in Section I.

Section II is an oscillographic study of the chief afferent cortical connections.

Foci responsive to audio frequency stimulation were demonstrated in the cerebral cortex of the dog. These foci occupy the middle ectosylvian gyrus (dorsal area), high frequencies located anteriorly, low frequencies posteriorly. Successive octaves were arranged at equal intervals along the cortex.

A ventral area possessing an inverse arrangement of frequencies and a higher threshold was demonstrated with frequencies of 100 to 400 concentrated upon the anterior ectosylvian gyrus, 8000 to 16,000 upon the posterior, and the intermediate frequencies dispersed over the sylvian gyrus and middle ectosylvian sulcus.

Each ear was represented bilaterally with the same pattern, but more strongly for the contra-lateral side.

Electrical stimulation of the bony spiral of the cochlea supports these observations.

In Section III, a third area responsive to tones and to electrical stimulation of the bony spiral was described, occupying the ventral extremity of the anterior ectosylvian gyrus. It was found bilaterally to electrical stimulation, but only unilaterally to tonal stimulation.

Severing the modiolus abolished the responses to electrical stimulation, and intracranial section of the 8th nerve abolished the responses to tones.

Ablation of the dorsal and ventral areas did not affect the responses.

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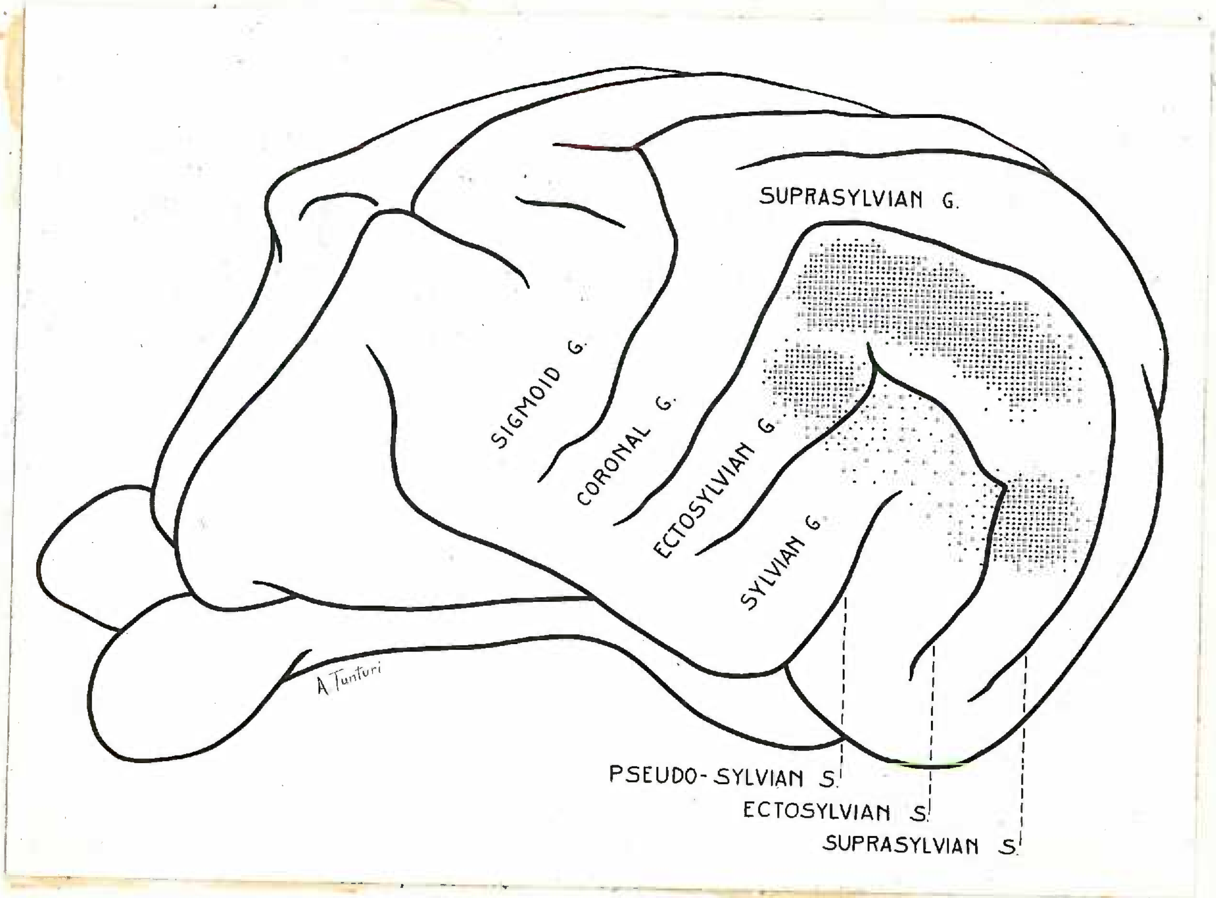
FIG. 1 -- Dorsal and ventral areas in the acoustic cortex of the dog in which localization to audio frequencies was demonstrated.

FIG. 2 -- Dorsal and ventral areas for frequencies designated at upper right. Right cortex; loudspeaker 0.75 meter from left ear; right cochlea destroyed. Only an occasional response from the sylvian gyrus. AEG, anterior ectosylvian gyrus; MEG middle ectosylvian gyrus; PEG, posterior ectosylvian gyrus.


SUPRASYLVIAN G.
SIGMOID G.
CORONAL G.
ECTOSYLVIAN G.
SYLVIAN G.
A Tunturi
PSEUDO-SYLVIAN S.
ECTOSYLVIAN S.
SUPRASYLVIAN S.

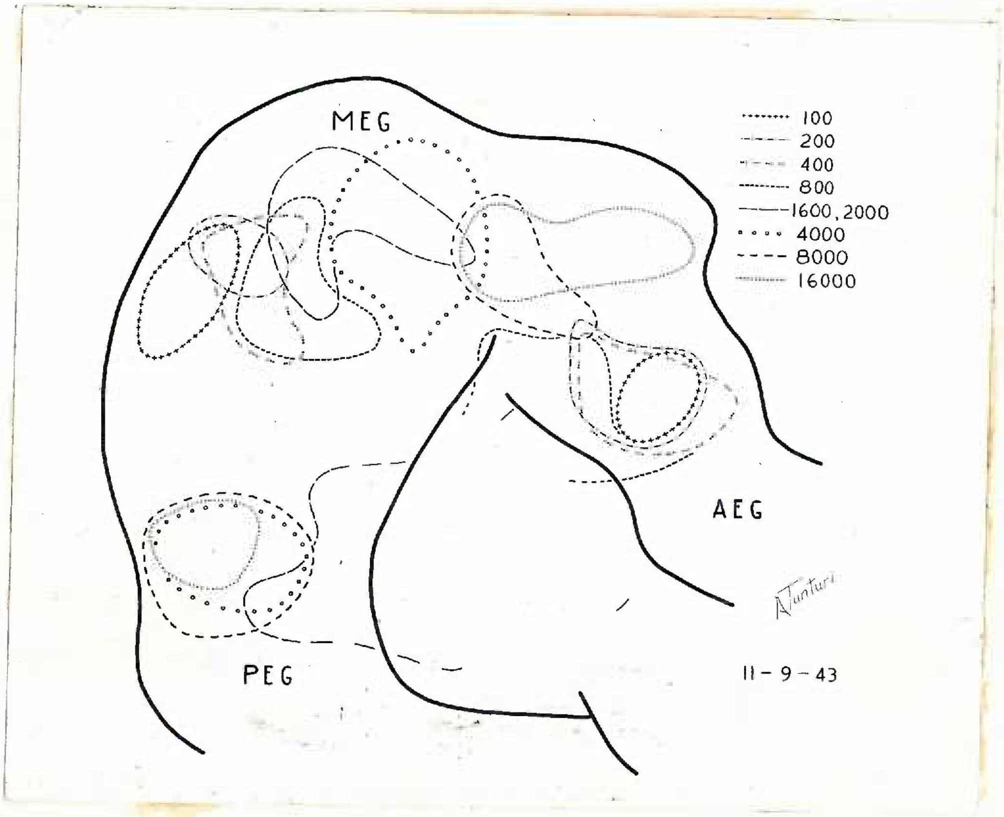
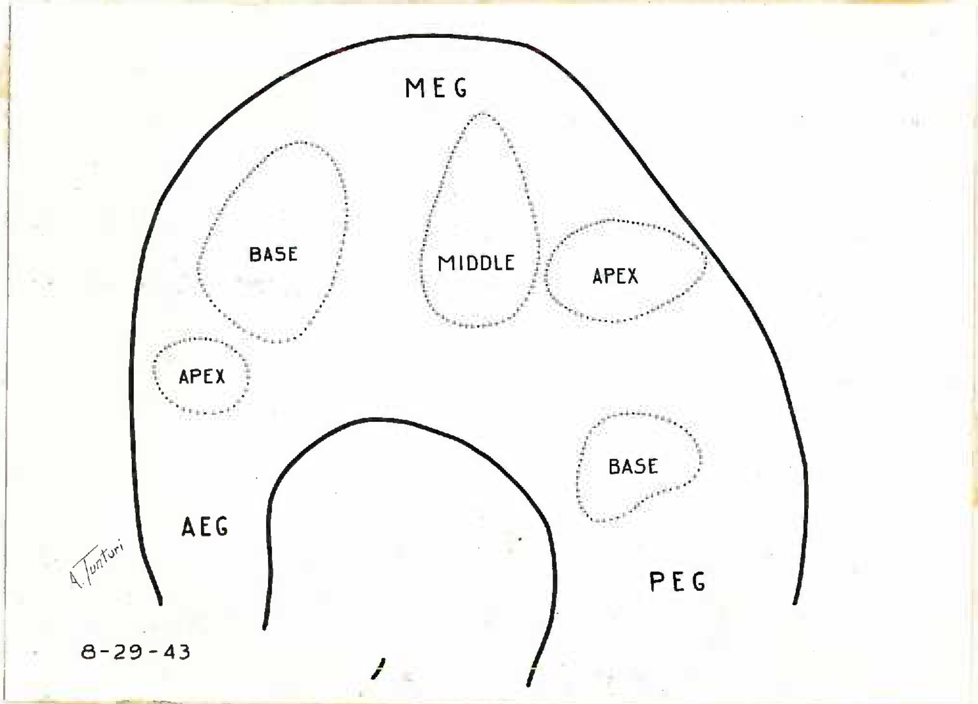
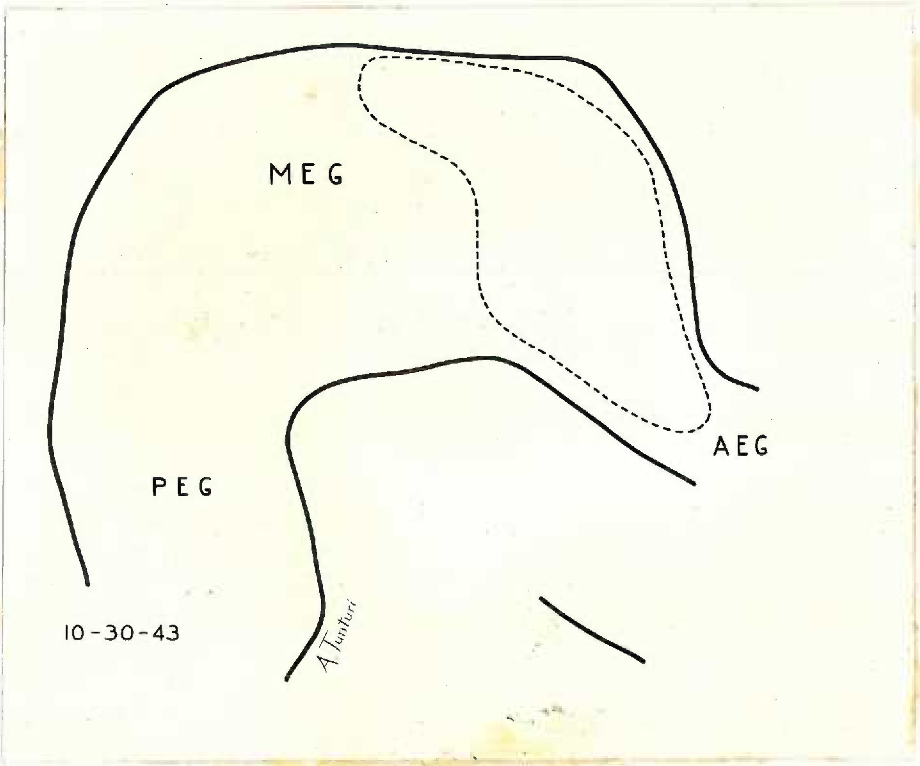

MEG
100
200
400
800
1600, 2000
4000
8000
16000
AEG
PEG
A Tunturi
11 - 9 - 43

FIG. 3 -- Area of the dog cortex from which initially negative responses were most consistently obtained.

FIG. 4 -- Left cortex. Left cochlear spiral stimulated at the ventral points of the apical, middle and basal turns. No responses from the sylvian gyrus.



8-29-43



10-30-43

FIG. 5 -- Maximum responses obtained from the various areas illustrated in Figure 2 to audio frequency stimulation. Left column: dorsal area. Right column: ventral area. The microphonic record of the sound is given below the cortical response except for 4000, 8000, 16,000 of the dorsal area and 800, 16,000 of the ventral area, for which the carbon microphone was insensitive particularly at low intensities. Time: 60 cps. Amplitude: 400 microvolts (for responses only). Downward deflection: surface positive.

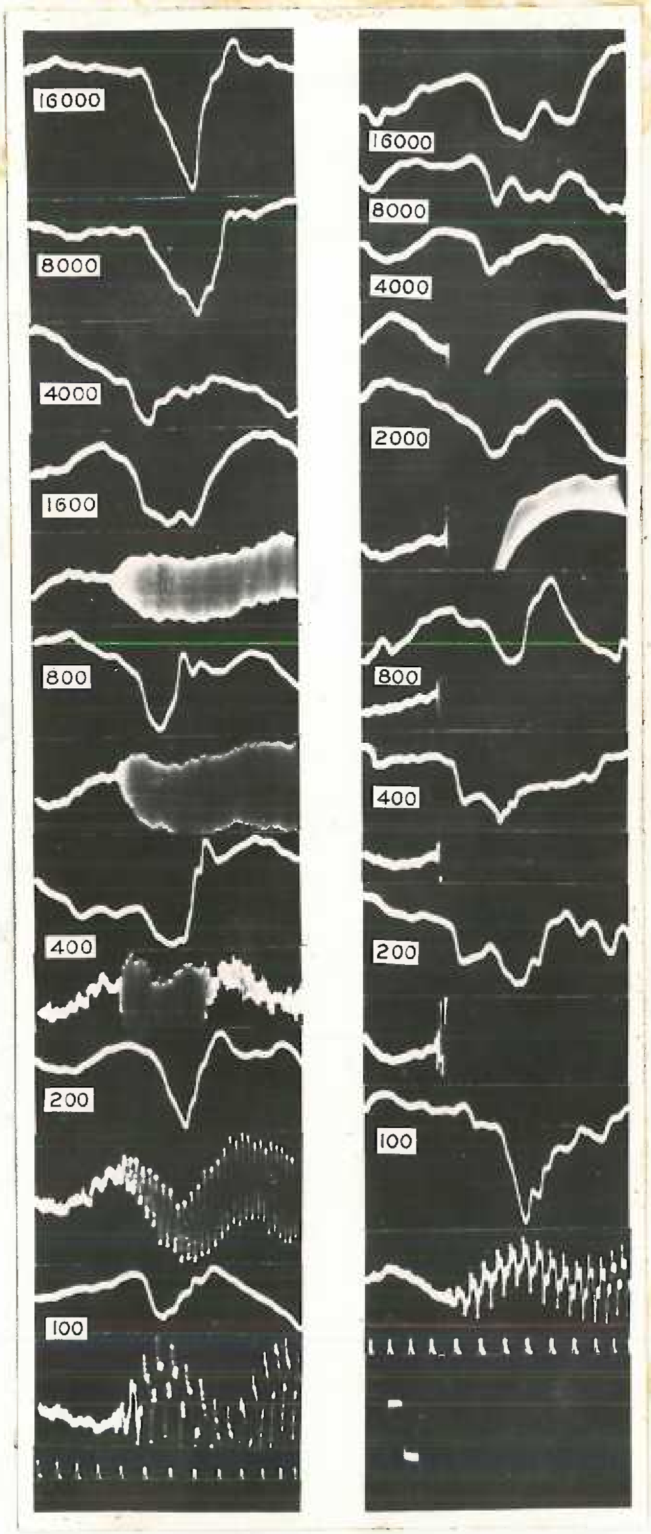
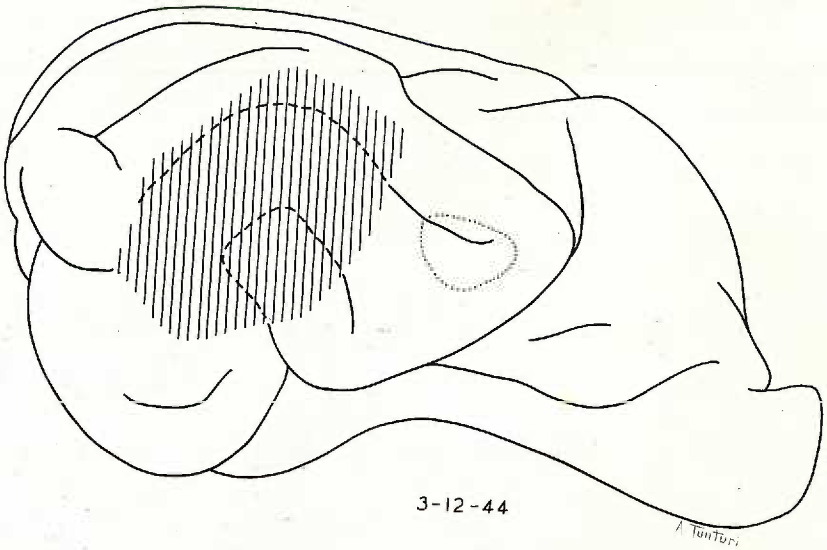

16000
8000
4000
1600
800
400
200
100
16000
8000
4000
2000
800
400
200
100

FIG. 6 -- The location of the responsive area on the anterior ectosylvian gyrus is shown in dotted line. The extent of ablation of the acoustic cortex which did not affect the responses is represented by vertical lines.



3-12-44

A. Tunturi

FIG. 7 -- Responses obtained in experiment of figure 6 to sound stimulation. Microphonic responses below for 500, 2000 and 4000 cps. Downward deflection: surface positive.

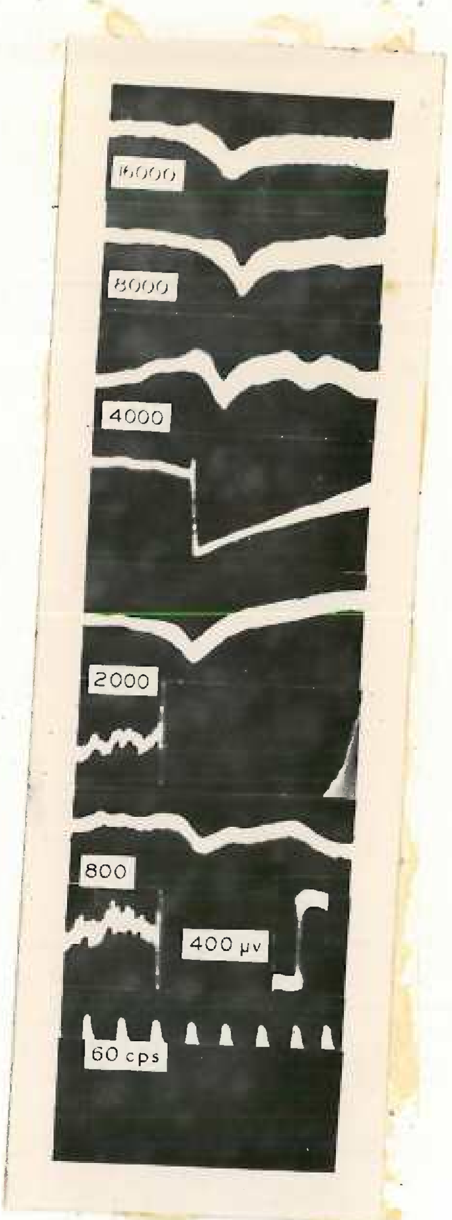
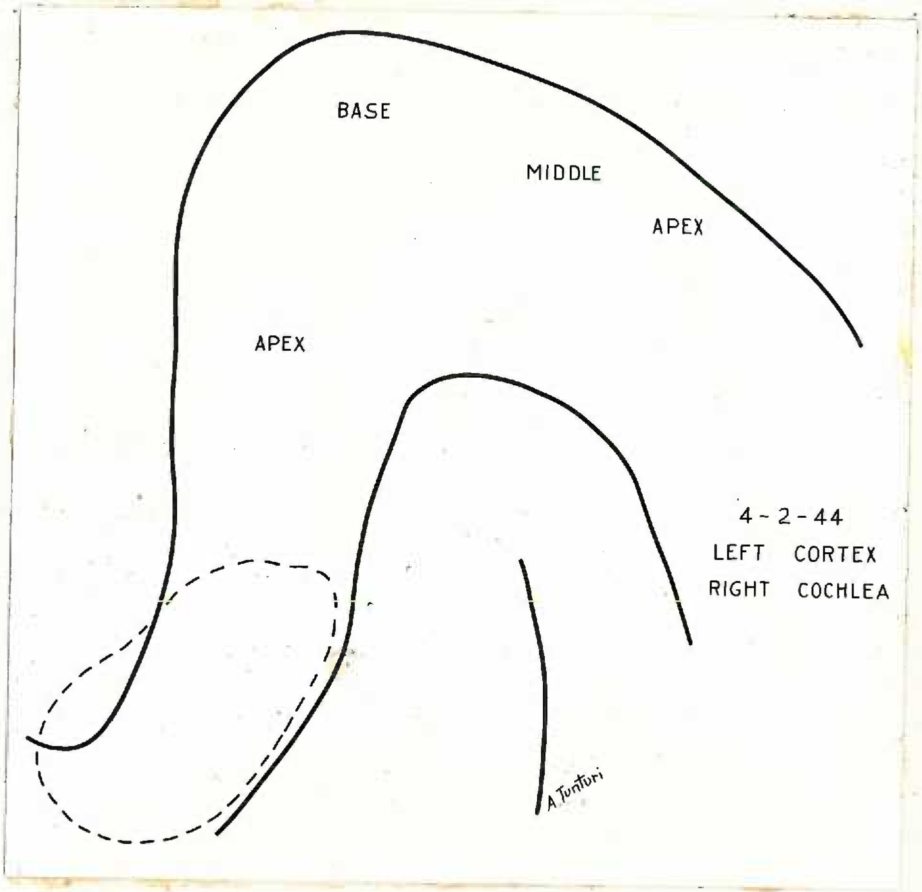

16000
8000
4000
2000
800
400 μv
60 cps

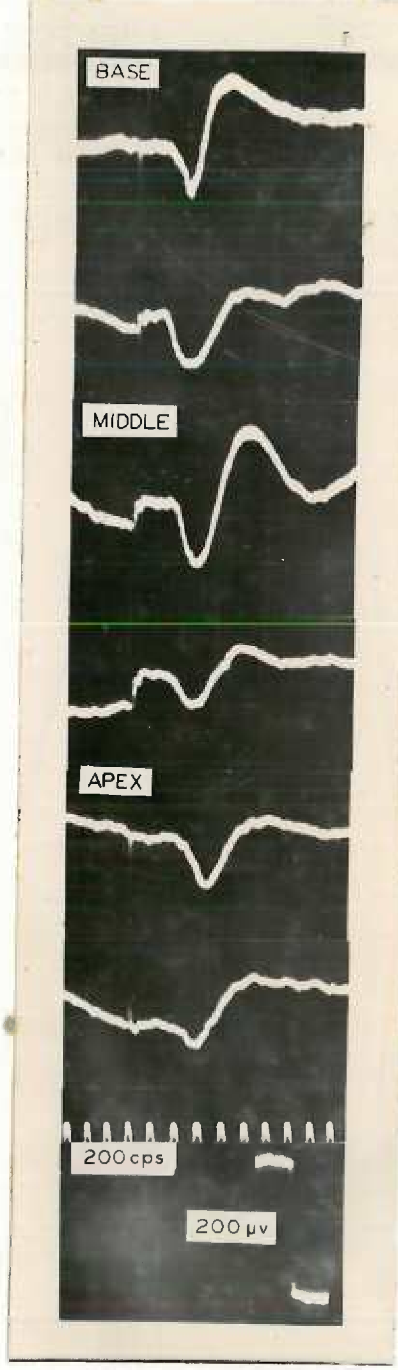
FIG. 5 -- Location of the responsive area to electrical stimulation of local regions of the bony spiral as related to the responsive foci of the middle ectosylvian gyrus and the apical region of the previously designated ventral area.



4 - 2 - 44
LEFT CORTEX
RIGHT COCHLEA

FIG. 9 -- Upper record of each pair obtained from respective focus on the middle ectosylvian gyrus in Figure 8. Lower record of each pair from the area on the ventral extremity of the anterior ectosylvian gyrus.

FIG. 10 -- Exp. 7/3/44. Similar records from ipsilateral side.


BASE
MIDDLE
APEX
200 cps
200 µv

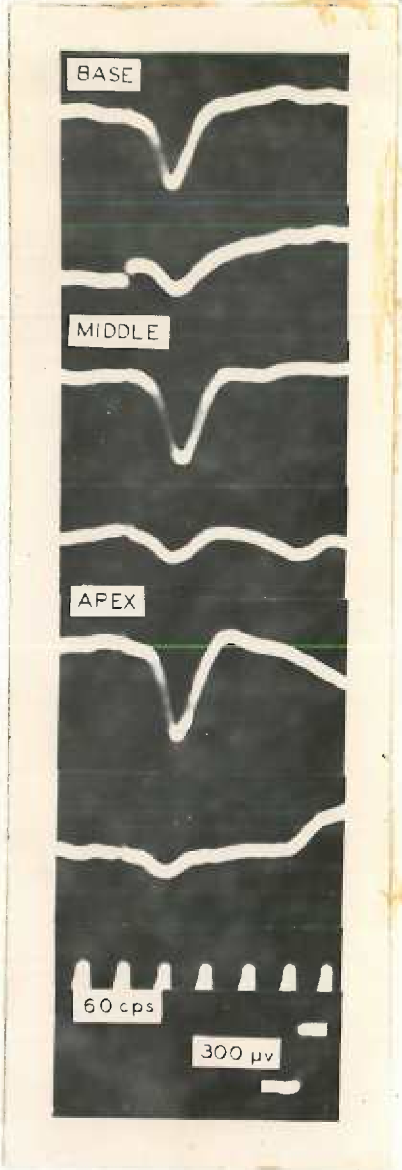
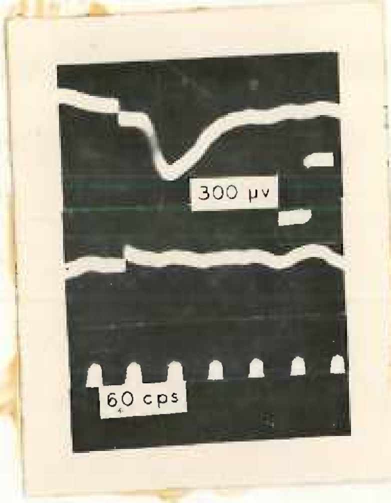
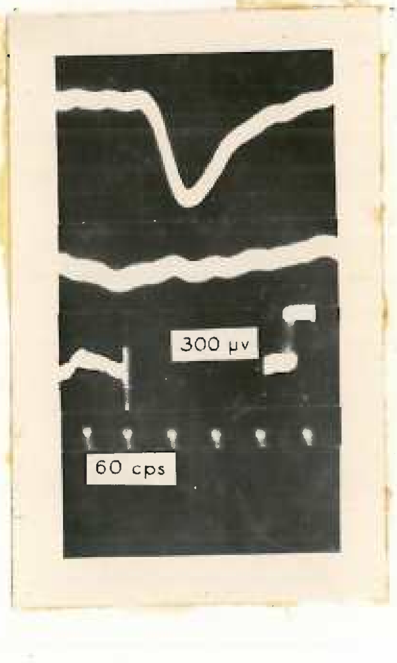

BASE
MIDDLE
APEX
60 cps
300 µv

FIG. 11 -- Exp. 7/17/44. Records from responsive area to electrical stimulation of the apical turn before and after severing the modiolus.

FIG. 12 -- Exp. 8/6/44. Record from area to stimulation with a frequency of 2600 cps. before and after section of the 8th nerve intra-cranially.


300 µv
60 cps


300 µv
60 cps