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OF A RESPONSE FIGURE

BY

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SURFACE MOVEMENTS OF CLICK RESPONSES FROM ACOUSTIC CEREBRAL CORTEX OF CAT: LEADING AND TRAILING EDGES OF A RESPONSE FIGURE[1]

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INTRODUCTION

EXPERIMENTS on the cerebral cortex of the cat with 25 implanted electrodes have indicated that the electrical activity contains certain forms or shapes which are called "figures" (3, 4, 5). Two parts of figures in acoustically responsive cortex resulting from single clicks are analyzed here in detail; attention is concentrated on the directions and the speeds of travel across the pial surface of the beginning and of the end of the base of the response figures[2] (6).

METHODS

Apparatus. The apparatus (3) consists of a square array of 25 electrodes, 5 by 5, 25 amplifiers, 25 glow tubes in a square array, and a motion picture camera. The electrode array (4) is constructed for implantation through the skull, and consists of 25 glass tubes imbedded in a lucite cylinder with their open ends placed flush with the end of the cylinder; their openings are spaced at 2 mm. intervals. The cylinder is mounted in a stainless steel barrel which has a tapered thread on its external surface; this barrel is screwed into a 0.75 inch diameter trephine hole in the skull. Small plastic tubes filled with normal saline lead from the glass tubes to 25 Ag-AgCl half-cells connected to the amplifiers. The 25 amplifiers (3) compute the instantaneous average potential of all 25 electrodes and deliver 25 output signals, each of which is equal to the potential difference between the mean potential and the corresponding potential of each electrode. Each amplifier has a time constant of about 1 sec., and a pass band 700 cps wide.

The 25 glow tubes are small, bright, capillary electrical glow-discharge tubes (Sylvania Company's type 1B59) viewed end-on, and are placed in a square array corresponding to the electrode positions. The light intensity of each glow lamp is adjusted with no signal coming from its amplifier to a definite, mean value (at about 9.0 mA. of current through the tube). Relatively positive signals decrease the intensity and relatively negative signals increase the intensity below and above this mean value.

The motion picture camera (Bell and Howell Superspeed Model 70) takes 128 pictures per sec. in the glow tube array. The frame cycle is thus 7.81 msec. in duration. The shutter is open six-tenths of this frame cycle.

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[2] In other papers, other parts of the response figures detectable at the pial surface are dealt with in some detail, as are the figures in the spontaneous activity.

Techniques. With the use of sterile technique and nembutal anesthesia at surgical depths, a circular hole is cut in the cat's skin over the site of the expected implantation of the electrodes; a purse-string suture of silk is placed around the hole. After removal of the periosteum and muscle, a 0.75 inch diameter trephine hole is cut through the skull. Bonewax is used to assure a blood-free field. With a dural hook and fine scissors the dura is removed and the arachnoid left intact. The cavity thus formed is filled with sterile normal saline. The sterile electrode array is screwed into the skull until sharp patterns of the electrical activity are seen on the glow tube array. The purse-string suture is tightened until the skin is held tightly around the stainless steel barrel. As a prophylactic measure, penicillin (100,000 units) is injected once per day for the first three days. The animal is placed in a sound attenuating enclosure with a small earphone about 6 inches in front of the face. A 50 μsec. pulse is fed into the earphone once every second to produce the high-pitched click. The amplitude of the pulse is adjusted to give just maximal cortical responses visible on the glow tube array. Dial anesthesia, supplemented with nembutal, is used over the subsequent days of the experiment. Sample records are taken at different anesthetic levels of the responses to clicks and, without intentional stimuli, of the spontaneous activity at approximately 1–5 hour intervals for four to seven days; since the activity did not change during this rather long period, it was not found necessary to give either saline or glucose intravenously.

Analysis. Records of a series of response figures are taken with the motion picture camera; after reversal development of the film, prints are made from the film by high-contrast photographic methods with careful control of the photographic parameters (5). These prints show the glow tube images as black spots on a white background. With no signal present, the black spots are of a certain size; with small positive signals, the spots are smaller and beyond a certain threshold value they disappear; with small negative signals, they become larger up to a limiting size. The sizes of the spots are used to select the areas of the array where there are positive, negative, and zero signals in each frame (Fig. 3, Ref. 5). In this paper the analyses were done on prints whose exposure was chosen to give maximum ease of selecting a positive and a negative relative change of about 25 μV. deviation from zero at the input of the amplifiers (5). During a response (such as those shown in Refs. 4, 5) the progress of a 25 μV. wave of differential potential change across the array can be charted and its position shown at times after the click corresponding to each frame of the record.

In order to achieve better time resolution than the 7.8 msec. frame cycle, an interpolation technique was developed. The records of a large group of responses which occurred in a given 20 sec. interval relatively free of spontaneous activity were chosen for analysis. The click occurrence was uncontrolled in its relation to the frame cycle. From an analysis of this group, it was found that the later phases of these responses were all practically identical in amplitude distribution on the cortex at similar times after the occurrence of the click. It was also noted that the earlier phases of the responses did not all look alike. By empirical matching, it was found that the group of records chosen for analysis could be arranged in a regular series according to the part of the frame cycle in which the click occurred. When this arrangement was completed, it was found that a definite sequence of frames had been set up which gives interpolated pictures of the orderly development and the orderly subsidence of the response figure at intervals of about a tenth of a frame cycle.

This interpolated series of frames is the basis for our analysis of the courses of the response figures presented in this paper. From the above sequence of frames, the latency of the arrival of the 25 μV. level at each electrode was determined for both the beginning and the end of the activity at each electrode. These latency values were placed in the electrode positions on a chart of the brain. For each group of four adjacent electrodes, the mean value of the latency was calculated. For the case of the first cat, this mean value was placed at the intersection of the diagonals of the square whose corners represented the positions of the four electrodes. Assuming that the 25 μV. level traveled at constant speed (but not necessarily in a constant direction) along any one side of the square or along any one half-diagonal between the center and each corner, the positions of integral values of latency on each of the eight lines of each square were calculated. The iso-latency lines were then sketched in by connecting these integral values' positions with smoothed curves.

In certain cases (one in the first cat and many in the second) there were not four electrodes available in a square or the four electrodes were at the corners of a simple quadrilateral, not a square. In these cases, the average value of latency was calculated for each

pair of electrodes, and placed on the halfway point between the pair on the line connecting them. Where possible the average of three or of four such averages of pairs was then placed equidistant from the position of the pair averages. All possible connecting straight lines were drawn; the positions of the integral values of latency were calculated along these lines; the iso-latency lines were then sketched in.

For the purposes of the analysis, activity (and hence the leading and the trailing edges) is defined as either a positive or a negative electrical change greater than 25 μV. from the zero signal value (5). All signals were found to be positive except in the case of two electrodes in the first and one in the second of the two cats presented here; these negative signals are symbolized by a minus sign in parenthesis (Fig. 1) and by an X (Fig. 2); all others are positive.

In each cat there are a limited number of electrodes resting on areas showing responses; in a subsequent paper an analysis of the spontaneous activity appearing under many of
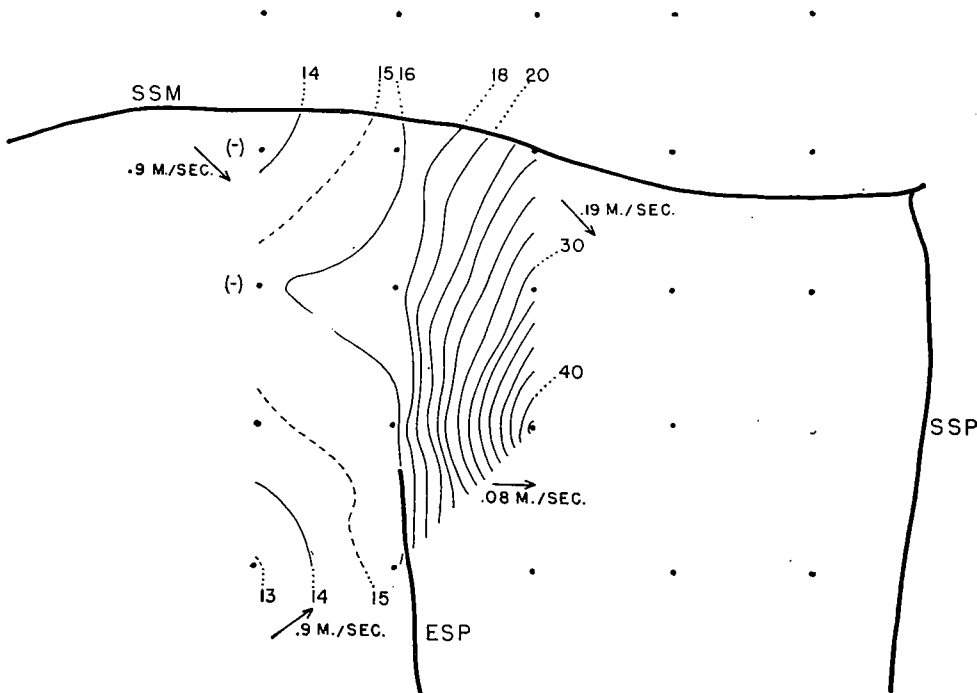

Fig. 1. *Positions and latencies of leading edge of a cortical figure of activity evoked by click (first cat, 271049).* In this and in all subsequent maps (Figs. 2–6) position of each electrode pore of array of 25 is shown by dot placed on brain diagram traced from photograph (3, 5). Important sulci are middle suprasylvian (SSM), posterior suprasylvian (SSP) and posterior ectosylvian (ESP). Eight responses were analyzed to give results from this cat (Figs. 1, 3, 5). Each plotted solid line is position of leading edge at the time after occurrence of click given at end of each line or of every fifth line in crowded regions; dashed lines are extra values in regions of high velocity (wide spacing, see text). All signals are surface-positive changes from resting value except where negative ones are symbolized by (—). Velocity of leading edge is given in certain places; its direction is symbolized by the arrow and its speed by the number near the arrow in m./sec. (M./SEC.); its place is region nearest arrow in chart where arrow can be placed and be perpendicular to lines denoting position of edge. Directions on brain used in text are "posterior" which is to right, "anterior" is to left, "up" is upwards, and "down" is downwards on this and all other charts.

the remaining electrodes will be presented; other electrodes across sulci allow control observations of related and unrelated activity in other, non-acoustic cortex.

In the first cat there are 11 electrode positions for the calculations (Fig. 1); for the second cat (Fig. 2) 21 positions were obtained from an array placement different from that in the first cat and by taking records at two array positions by rotating the array in the skull.

RESULTS

The results from two cats (Figs. 1–6) present three functions plotted on the surface of the cortex: the instantaneous positions (a) of the beginning, (b) of the ending, and (c) of the durations of the activity at 2 msec. intervals. The beginning of the activity is called the "leading edge" of the figure
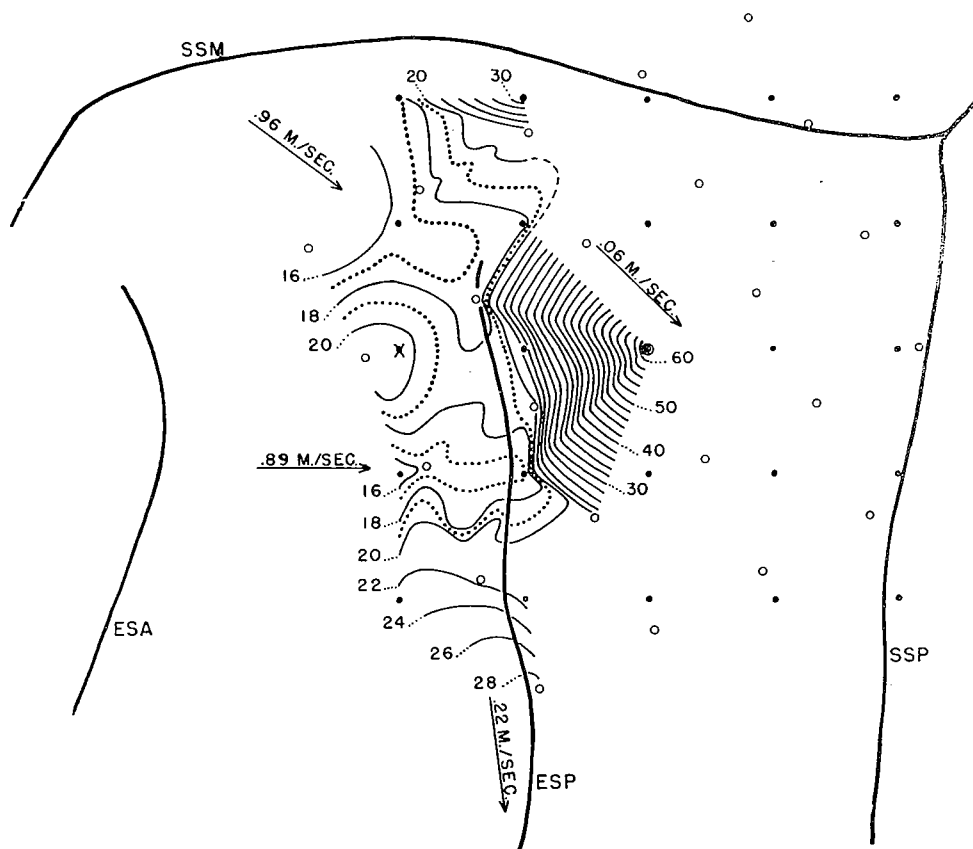

FIG. 2. *Positions and latencies of leading edge in second cat (191149).* On this chart, two electrode array positions are shown, first by dots, second by small circles. Twenty responses were analyzed, ten for each array position. One electrode, center one, is common to both array positions, and is shown by encircled dot. Negative signals were seen at one electrode which is marked with X. All other symbols are as in previous chart (Fig. 1) with the addition of anterior ectosylvain sulcus (ESA). Continuation of high velocity of leading edge beyond posterior ectosylvian sulcus is probably an artifact: there is no set of electrodes on cortex anterior to sulcus which is close enough to give a more accurate measure of position of speed change (text).

and corresponds to about a 25 μV. increase in potential difference away from the level with no signal present (Figs. 1, 2); the end of the activity is called the "trailing edge" of the figure and corresponds to a decrease in potential toward the level with no signal present (Figs. 3, 4). The differences between the latencies of the leading and of the trailing edges at each cortical point gives the duration of the activity, and hence the time spent by the response figure in traversing that point (Figs. 5, 6).

Since the plots of the positions of the leading and the trailing edges give position, direction, and time, the velocities of these edges at different places can be calculated directly from the plots. The farther apart the positions of the lines occur in adjacent 2 msec. intervals, the faster the edge is moving. The direction the edge is moving is, in general, perpendicular to the iso-latency line designating the position and is directed toward the next line occurring later. For example, in our first cat the leading edge (Fig. 1) enters and traverses the upper left and lower left part of the array at about 0.9 m./sec. and later slows to about 0.19 and 0.08 m./sec. as it crosses the array: the arrows show the direction in which the velocity was measured.

Leading edge. The leading edge of the response figure signifies the beginning of the activity for the given instant after the click. The leading edge
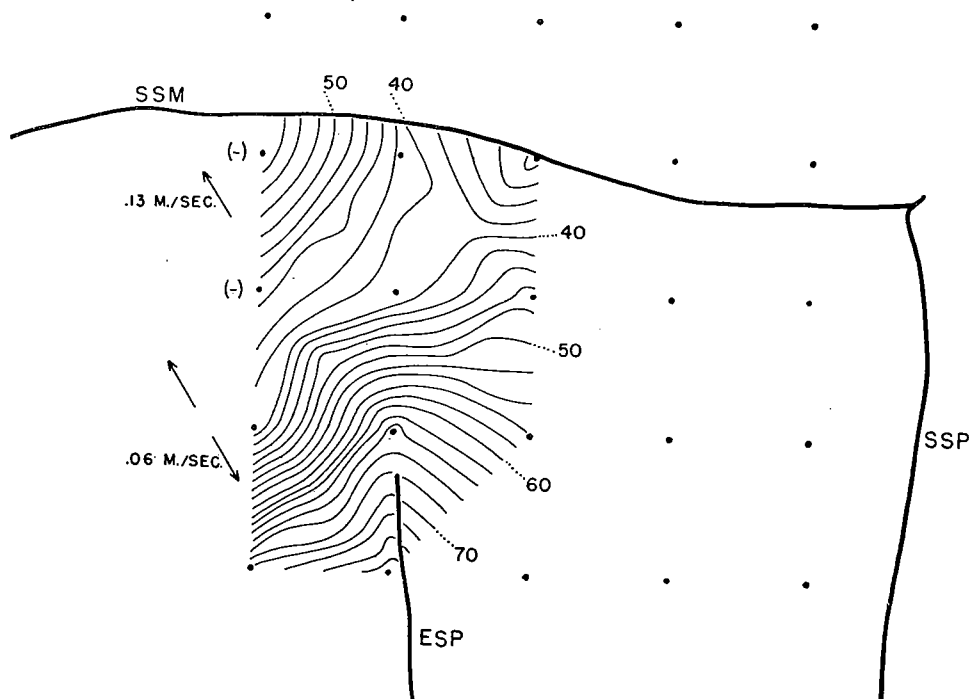

FIG. 3. *Positions and latencies of the trailing edge of response in first cat.* Line of split after 38 msec. (see text) between downward and upward moving trailing edges lies between the two 40 msec. lines; its anterior end is shown by two arrows at left pointing in opposite directions.

in both cats (Figs. 1, 2) shows at least two major regions of grossly different velocity of travel; the division between these two regions is approximately the posterior ectosylvian sulcus (ESP) and a line extended dorsally from this sulcus to the middle suprasylvian sulcus (SSM).

In the first region, anterior to this dividing line (to the left in Figs. 1, 2), the latencies range from 13 to 16 msec. (first cat) and from 15 to 18 msec. (second cat); the velocities range from 0.89 to 0.96 m./sec. In this first region in both cats there are two places at which the leading edge strikes the array first, a dorsal and a ventral one; the latencies after the occurrence of the click at these places range from about 13 msec. to almost 16 msec. It cannot be stated definitely that these are two separate origins for the leading edge: they may represent two parts of an irregular front approaching the array in such a way as to strike these particular electrodes first. After once entering
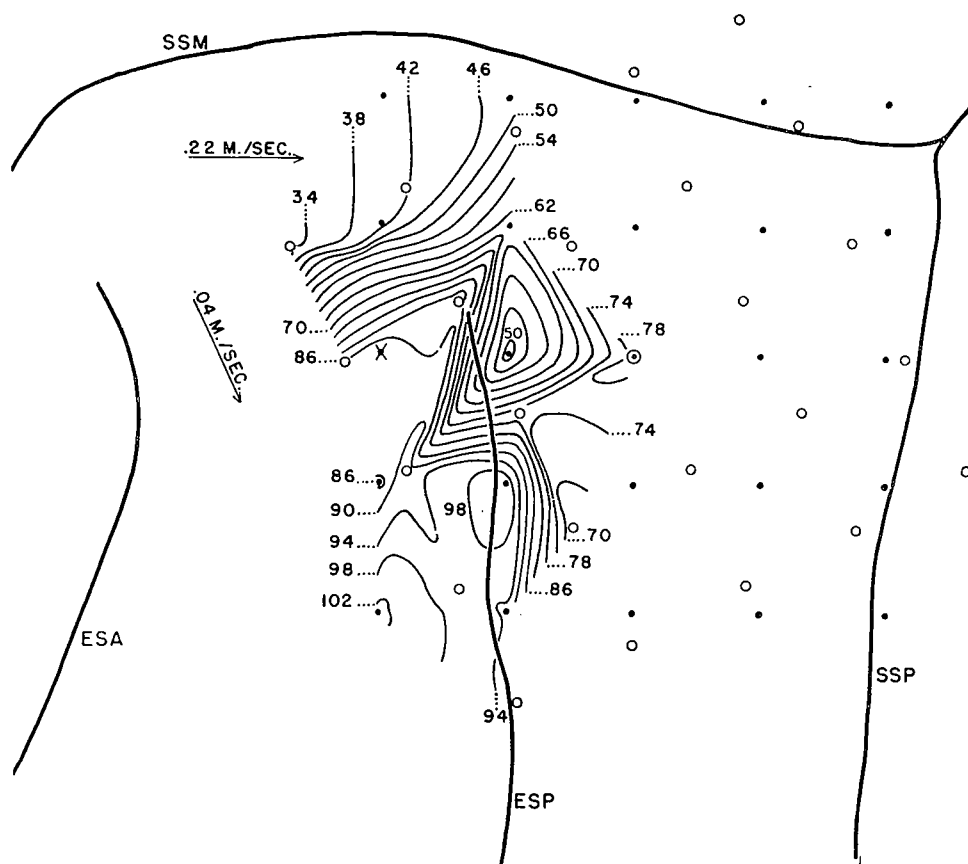

FIG. 4. *Positions and latencies of trailing edge in second cat.* Trailing edge moves predominantly downwards; another trailing edge appears at 50 msec., forming a "hole" in the active region just posterior to posterior ectosylvian sulcus (text). Some of irregularity of trailing edge along posterior ectosylvian sulcus probably is due to cortex bending at and contained within sulcus.

the array, the two separate leading edges in each cat sweep across the anterior region and join into one edge just before they reach the boundary between the anterior and the posterior regions (16–17 msec. for the first cat and 18 msec. for the second cat); at or just before this boundary, there is a rapid deceleration of the edge to a lower velocity in the posterior region (17–42 msec. in the first cat and 19–60 msec. in the second).

Due to the presence of the sulcus (ESP) and of the electrodes anterior to this sulcus, the determination of the position of the boundary of deceleration is not definite in the second cat: the boundary probably lies within the sulcus (Fig. 2). The data from the last group of six active electrodes which lie just on and behind the posterior ectosylvian sulcus show the same low velocity for many responses. In this low-velocity, posterior region, the frequency with which responses penetrate to a given distance posterior to the sulcus decreases with increasing distance: about 90 per cent of the responses reached the above mentioned six electrodes, only two out of the 20 reached the center electrode, and none reached the other electrodes which lies posterior to the center one.

In the second cat, the leading edge shows a number of features (Fig. 2) not seen with the first cat (Fig. 1). Both the upper and the lower parts of the first region (anterior to ESP and its prolongation dorsally) show a region of slowing of the edge; both the upper and the lower one indicate two other boundaries with velocity changes for the leading edge. The two beginnings of the leading edge show a peculiarity in the region of the electrode marked with an X: this electrode showed negative signals (the central 20 msec. isolatency line in Fig. 2).

In summary of the main findings on the leading edge of the response to a click, there are possibly two origins (ventral and dorsal) and at least two regions characterized by different velocities of travel, an anterior, high-velocity one and a posterior, low-velocity one; the boundary between these two regions is close to the posterior ectosylvian sulcus and its prolongation toward the middle suprasylvian sulcus.

Trailing edge. The trailing edge of the response figure (Figs. 3, 4) does not show the orderly sequence of positions seen for the leading edge (Figs. 1, 2). The boundary between the anterior regions of the high-velocity leading edge and the posterior low-velocity region is not visible in the movements of the trailing edge. In the case of the first cat (Fig. 3) the trailing edge starts moving out of the active region at 32 msec. after the click in the upper and most posterior active electrode near or on SSM; this is about 10 msec. before the leading edge has reached the last electrode to become active (Fig. 1). The trailing edge moves downward and anteriorly from the 32 msec. position to the 38 msec. position; at this time a split occurs in the trailing edge: by 40 msec. there are two trailing edges, one moving upward and forward, and one moving downward. The edge moving upward is in the region of negative signals; the downward moving edge in its anterior part is slower (about 0.06 m./sec.) than the upward moving one (about 0.13 m./sec.).

In the case of the second cat (Fig. 4), the trailing edge shows a rather

complex course across the cortex. As in the first cat, the edge starts out of the region at about 34 msec. after the click which, again, is before the leading edge has penetrated fully into its posterior, slow-velocity region (60 msec. at farthest measurable point). The general direction of the movement of the trailing edge is downward, leaving the array at 102 msec. after the click. The intermediate course is rather complicated; a hole appears just behind the posterior ectosylvian sulcus at 50 msec., a part moves off the posterior point of the active region at 78 msec., the negative electrode region (X) is skirted rapidly, and another hole develops farther down the sulcus at 98 msec. It is to be noted that the hole at 50 msec. develops before the leading edge has moved to the farthest posterior limit (60 msec., Fig. 2). Though the trailing edge's speed is about 0.04 m./sec. over a large fraction of the area, at least two regions of higher speed are seen at the upper end of the active region (0.22 m./sec.) and at the lower end (0.1 to 0.2 m./sec.).

Comparison of directions of travel. If the charts for the sequential positions of the leading and of the trailing edges are superimposed for each cat separately, it is found that the two sets of iso-latency lines tend to lie at
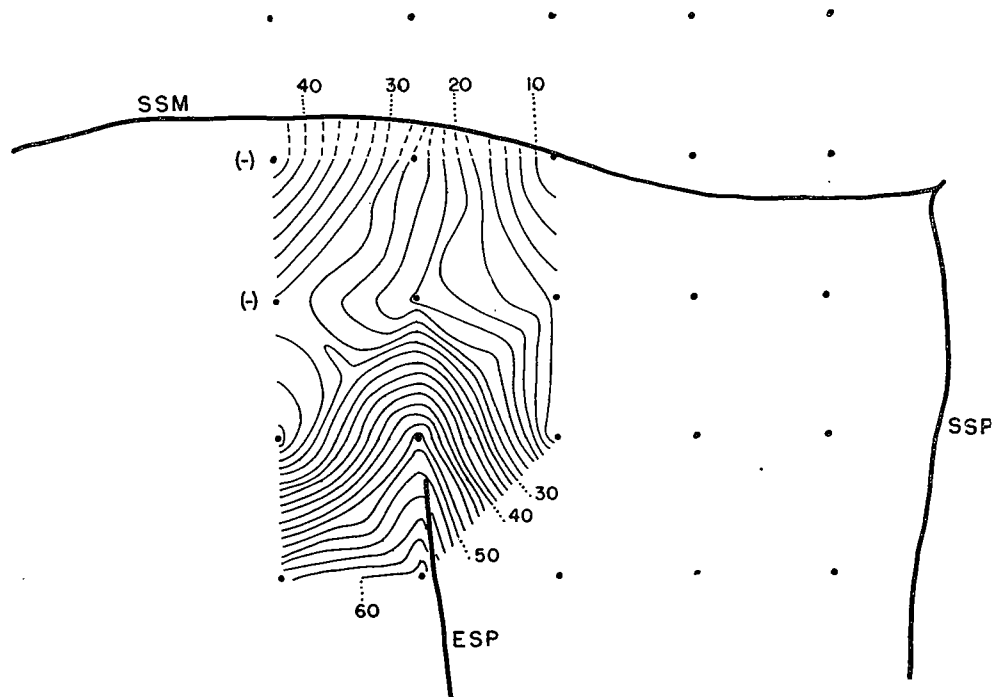

FIG. 5. *Durations of activity in first cat.* In contrast to the four previous charts (Figs. 1–4), in this one the lines symbolize regions of equal duration of activity instead of latency of arrival after click. Numbers at ends of lines give duration in msec. Durations given here are elapsed time, point-for-point on cortex, between time of arrival of leading edge and that of trailing edge (see text). Shortest duration shown is 10 msec. (upper right), longest is 60 msec. (lower center).

angles to each other nearer 90° than 0° or 180°. The only sizeable region of exceptions is at the upper and anterior parts of the active region in the first cat: in this region of the surface-negative signal, the two sets of lines tend to be parallel. In other words, except in a region showing relatively surface-negative activity, the trailing edge tends to move over the cortex in directions which approach angles close to 90° to the directions taken previously by the leading edge.

Durations. The duration of the activity at each point of the cortex is obtained by calculating the elapsed time between the arrival of the leading edge and that of the trailing edge at each point (Figs. 5, 6). Due to the relatively high velocity of the leading edge and the relatively slow velocity of the trailing one, these charts resemble those for the iso-latency lines of the trailing edge.

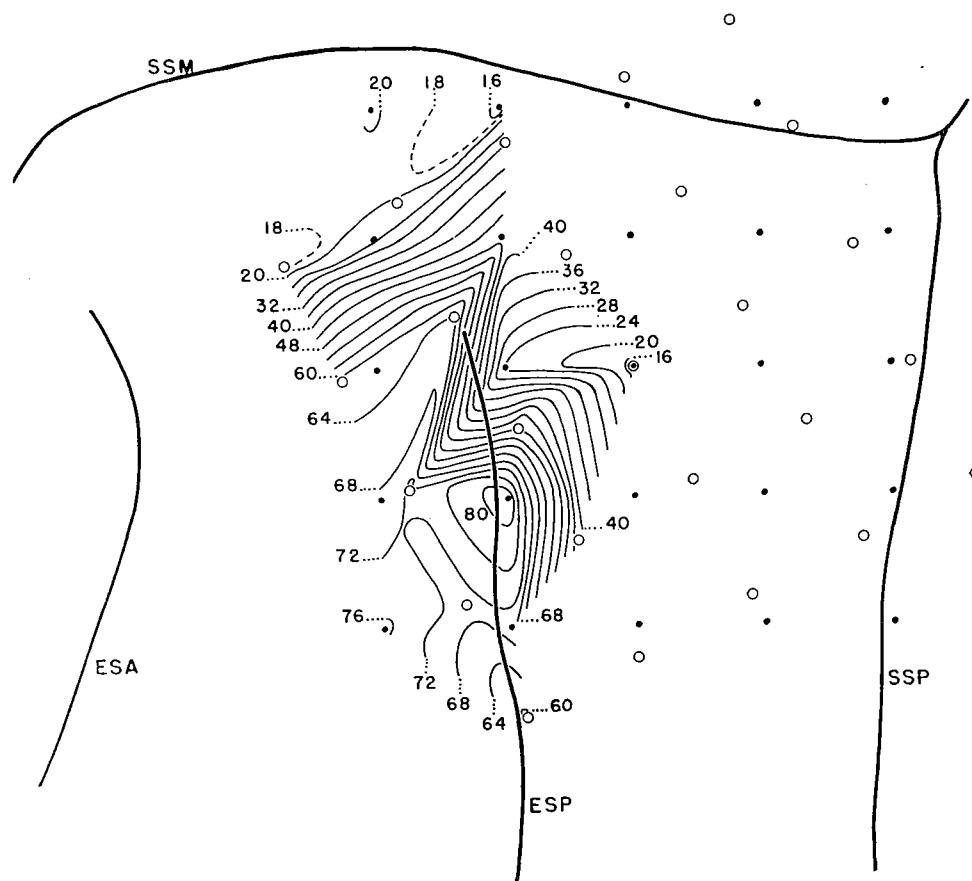In the first cat (Fig. 5), the shortest duration of activity (10 msec.) cor-

Fig. 6. *Durations of activity in second cat.* Shortest duration of activity is 16 msec. (top and to right), longest 76 and 80 msec. (center near bottom and bottom left).

responds to the first zone from which the trailing edge moves; the longest duration is found in the last zone from which the trailing edge moves (Fig. 3); these two zones are, respectively, at the upper right and at the lower middle parts of the active region. The durations tend to increase in the same directions as the trailing edge moved. The gradient of duration change over the cortex varies from about 3 msec./mm. (upper middle part) to 16 msec./mm. (lower part).

In the second cat (Fig. 6), the short durations cluster near the upper left part of the active region and near the farthest point penetrated posteriorly; the longest durations are at the lower end of the active region: one of 80 msec. and one of 76 msec. In general, as in the first cat, the durations tend to increase in the directions taken by the trailing edge as it traveled. The gradient of duration change over the cortex varies, in regions not containing the sulcus (ESP), from 8 to 32 msec./mm.

DISCUSSION

The leading edge of a figure of a click response moves very rapidly (about 1 m./sec.) in a definite region of the cortex and slows down rapidly at a definite boundary (Figs. 1, 2). The region of high velocity corresponds to the posterior part of acoustic I and II of Rose (7) more closely than to that of Rose and Woolsey (8) or of Woolsey and Walzl (9); the region of lower velocity lies in the anterior part of Rose's posterior ectosylvian area (7). We interpret this change of velocity at the boundary to mean that there is a structural change in the cortex, in cortical-subcortical connections, or in both at this boundary. Rose (7) gives anatomical evidence for a change in cortex and in subcortical connections at this boundary: acoustic I and II can be distinguished from the posterior ectosylvian and from one another by cytoarchitectonic inspection; acoustic I receives the direct afferent fibers from medial geniculate; acoustic II is suspected of receiving a separate, at present unknown, afferent supply; there is no known afferent projection to the posterior ectosylvian region; the cortical-cortical connections are yet to be delineated. In the light of the above known and postulated connections for acoustic I and II, the high-velocity leading edge is probably due to a preformed afferent figure moving up to cortex from below, firing the cortical cells first anteriorly and later posteriorly. Thus the leading edge reflects sequential firing of cortex by impulses coming into cortex at different times at different places: the "velocity" of the leading edge reflects these differences.

However, at the posterior boundary between the high- and the low-velocity regions (acoustic I and II, and posterior ectosylvian regions), it is probable that the velocity change reflects a change from the afferent determining of "velocity" to a cortical one: the slow leading edge is due to cell-to-cell firing within cortex alone in the posterior ectosylvian region. The velocities found in this region correspond, within a factor of 0.5 to 1, to the surface-positive response to direct electrical stimulation of intact (1) and of

isolated cortex (2). This cortical response moves from the stimulated region as a non-decrementing wave; waves like this one can also be elicited either by afferent activity arriving at a small region of acoustic cortex, or by a cortical tissue bridge to the isolated cortex (2).

The close correspondence in range of surface speeds between the slower leading edge (Figs. 1, 2) and that of the trailing edge (Figs. 3, 4) suggests that late in the activity some purely cortical system has been excited, a system similar to that giving the surface-positive response of Adrian and Burns (1, 2). Further, since all trace of the above boundary disappears in the charts of the trailing edge (Figs. 3, 4), it is suggested that this cortical system extends across the boundary between acoustic I and II, and the posterior ectosylvian region; and that there is little, if any, change in this system at the boundaries of the three anatomical regions. Local differences in the timing and in the number of cells fired by the afferent figure may explain the irregular directions and local speed differences of the trailing edge in our charts. The predominating tendency of the trailing edge to move downwards across the three anatomical areas may reflect a more or less uniform structural gradient (7) of the number of connections or of the cellular density in this cortical system.

The observation that the trailing edge tends to follow courses nearly at right angles to those taken by the leading edge irrespective of speed differences is yet to be explained satisfactorily; further experiments may allow a more definite choice among alternative explanations involving directions of current flow resulting from figures of activity in sheets of connected neurons, excitability and recovery cycles, number of active units in each area at each time, and structural factors.

Summary

By means of a recording technique which gives simultaneous samples of the electrical activity from 25 electrodes on the cerebral cortex, records of click responses are taken on the acoustically responsive cortex of cats. Results are presented of analysis of such responses. The parts of figures occurring in the responses which are analyzed in this paper are the leading and the trailing edges, which represent times near the beginning and near the ending of the cortical activity at each cortical point, respectively. The charts (Figs. 1–6) show the positions (a) of the leading and (b) of the trailing edges at 1–4 msec. intervals over about the first 100 msec. after the click, and (c) of lines of equal duration of cortical activity. It is found that the leading edge moves at a high velocity (about 1 m./sec.) in a region corresponding to the generally accepted projection areas (acoustic I and II) for the acoustic system. The leading edge suddenly slows (18 msec. after the click) at a definite boundary to about a tenth of its previous velocity in a region corresponding to the posterior boundary of acoustic I and II and the anterior edge of the posterior ectosylvian region. In contrast, the trailing edge moves over the active region at velocities about those of the leading

edge after it slows down posteriorly, and shows no unique changes in direction or speed in the vicinity of the anatomical boundary between acoustic I and II, and the posterior ectosylvian region.

It is concluded (i) that the leading edge, in the projection area, reflects the magnitudes and the timing of parts of a preformed afferent figure exciting cortex at different places at different times, (ii) that the leading edge in the posterior ectosylvian area represents activity of cortical cells only, and (iii) that the trailing edge represents later activity of a cortical system which exists throughout the three anatomical areas; this postulated cortical system has no definite boundaries within the three areas, but probably has a gradient of structural change running predominantly from top to bottom of this region of the cat's cortex. The resemblance of this latter system to that giving surface-positive responses to direct electrical stimulation of cortex (1, 2) is discussed.

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