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SURFACE MOVEMENTS OF FIGURES IN SPONTANEOUS ACTIVITY OF ANESTHETIZED CEREBRAL CORTEX: LEADING AND TRAILING EDGES[1]

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INTRODUCTION

EXPERIMENTS using a method of recording from 25 electrodes simultaneously give indications that the spontaneous electrical activity under anesthesia contains definite patterns called "figures" (6). The preceding paper (7) on click response figures gives an analysis of the positions, speeds, and directions of travel of the leading and of the trailing edges; in the present paper, a similar analysis is given for some spontaneous figures found in the posterior ectosylvian gyrus. At present, the spontaneous figures cannot be specified in the definite way that the response figures can be; unknown factors not under the control of the observer determine their time and place of occurrence (6). The present analysis is a statistical one; the results are shown in charts of the most frequent behavior of a group of spontaneous figures.

METHODS

The apparatus, the technique of recording, the method of making prints from the records, and the way in which data for analysis are obtained from the prints are presented in the preceding papers (6, 7). In the case of the analysis of the responses (7), the courses and times of occurrence of the leading and the trailing edges of the response figures were sufficiently reproducible from one response to the next in a long series to permit an interpolation technique for constructing the charts. In the case of the spontaneous figures, there is no such stereotyped reproduction of origins, courses, and velocities (6: Figs. 8, 9); a technique of analysis more suited to the variable nature of the spontaneous figures is used. The results presented in this paper are from the first cat in the preceding paper (7) on responses.

For the analysis, during a time in which no intentional stimuli were introduced, a single long segment of record of 3200 frames was selected; this segment records the spontaneous activity occurring in 25 sec. The anesthesia is nembutal, and is presumably at a very constant level because of the short time of the recording and the absence of detectable disturbing stimuli. The level chosen was slightly lighter than that which is used to obtain responses free of spontaneous figures, but deep enough so that a large fraction of the spontaneous figures are large and slow (6). At lighter levels, the figures travel too rapidly for adequate analysis with the present time resolution of the technique (6).

In this long segment of record, 27 spontaneous figures were found and printed (6:

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Figs. 8, 9). Of the 27 figures, 20 were selected for analysis: the criteria for selection are arbitrary ones best seen by comparing the 20 selected figures with the seven rejected ones; the accepted ones are those with the largest amplitudes, the largest area of maximum extent, the slowest speed, and the longest time spent in the array. Using these criteria, it was found that there were five figures which were eliminated unequivocally, and two borderline cases. Of the seven which were eliminated, the first two were in the camera's acceleration period and were considered not accurately timed (frames 16 and 119); two were too small to be considered as significant (frames 2868 and 2951); one was moving too rapidly and the record contained some ambiguous activity across the middle suprasylvian sulcus (frame 964); the two remaining figures (frames 907 and 2021) were eliminated as borderline cases; they may or may not be included under the above criteria.

After selection, each of the 20 figures was mapped in time and in space on the array. In contrast to the case of the responses (7), only the relatively positive parts of the figures were measured; the boundary between missing (relatively positive signals) and black (zero or relatively negative signals) images is timed and placed for each frame of each figure. This procedure is indicated by the fact that this boundary stands out in each figure as the one which tends to be closed, allowing for the fact that the figure may intersect the array's outer limits. In a later paper all parts of a typical figure which lie within the array are measured and charted as equipotential contour maps; those results also indicate that the relatively surface-positive parts of these figures give the major features of their history; no large closed boundaries around negative peaks are seen in the spontaneous activity. The selected boundary represents about a 25 μV. change in the relatively positive direction from zero relative potential.

In detail the measuring technique for each figure is carried out frame by frame by first establishing an arbitrary zero time for that figure. By inspection of the prints of the sequence of frames for the figure, the region of missing images is followed back in time to that frame first showing one or more missing images which can be unequivocally assigned to that figure: the time halfway between this and the just preceding frame is taken as the zero of the time scale for this particular figure. From that point on, the time scale is given by the 7.8 msec. frame cycle (6, 7) multiplied by the number of frames from the zero time. The first step in the analysis of the course of the leading edge of the figure is to place on a brain chart at the given electrode (glow tube) position the time (in msec.) after zero time at which that image disappeared from the array. On another brain chart is placed the time at which the image is seen again; these numbers are later used to plot the course of the trailing edge. For the 20 figures, there are 20 such charts for the leading edge and 20 for the trailing edge. These charts are analyzed in several ways and the results are plotted on brain maps (Figs. 1–7).

The analysis is begun by averaging at each electrode locus the times of arrival of the leading edges of all 20 figures. These average times are placed on a brain chart of each electrode locus. By the method outlined in the preceding paper for the leading edge of the response figures (7), the position of an average leading edge for each integral value of time after the arbitrary zero time is found and sketched in (Fig. 1). By limiting the choice in the averaging calculation to the first 78 msec. (10 frames) of the figure, a chart of another type of average leading edge is constructed (Fig. 2). In a manner similar to that for the first leading edge the positions of an average trailing edge are found (Fig. 3). By calculating the difference in time at each locus between the average trailing and the first of the above average leading edges, the average duration of activity at each point is calculated and is plotted for the integral values (Fig. 4). In the last part of the analysis, the statistical frequencies within the group of 20 figures for three variables are calculated: the number of figures whose leading edge arrives at each point first, the number whose trailing edge leaves each point last, and the number which includes each point at their maximum extent within the array. These numbers are determined by counting, for each electrode, the figures which have the property in question, and, in the usual manner, determining the position on the cortex of the integral values (Figs. 5, 6, 7).

Results

The results of the analysis of the selected set of 20 spontaneous figures are shown in two groups of charts; the first group (Figs. 1–4) shows the

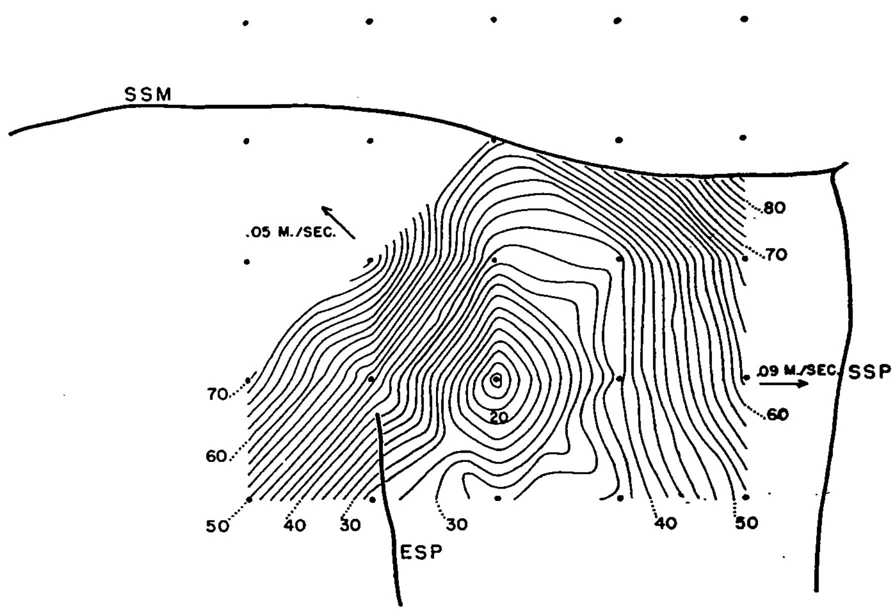

FIG. 1. *Sequential positions of an average leading edge for spontaneous figures.* Beginnings of leading edge center around two electrodes just posterior to tip of posterior ectosylvian sulcus (ESP) at 16 msec. and at about 26 msec. after the arbitrary zero time; this is region of anterior origin for figures (text). Minimum velocity (0.05 m./sec.) region is just above this origin; maximum velocity (0.2 m./sec.) region lies in upper center of active region. This map includes travel of leading edges from both origins (Fig. 2) all the way across array; later chart (Fig. 2) shows only first part of this travel; overlapping courses of many figures appear in above averages (Fig. 5).

positions of two averaged leading edges (Figs. 1, 2), one averaged trailing edge (Fig. 3), and the averaged durations of the activity at each point (Fig. 4); this group gives the same variables that were shown for responses in the preceding paper (7). The second group of charts shows the variation within the population of figures of the zones of origin or of entry of the leading edge (Fig. 5), of the zones of die-away or of exit of the trailing edge (Fig. 6), and of the zones of maximum extent of the figure's boundary within the array (Fig. 7). Only 15 electrodes are touched by all of the figures; none cross the middle suprasylvian sulcus.

Origins and leading edge. Of the two ways (Methods) of obtaining an average set of positions for an average leading edge, the first way gives a picture (Fig. 1) which includes the travel zone beyond the region of entry: each leading edge comes into the array either from outside the array (entry) or within it (origin), and travels across the array. In the first averaging process, the travel across the array of certain figures is averaged in with the origin or entry of others; the result is a very much smoothed picture of the positions of an average leading edge. The averaged velocities (calculated as in 7) are found to be within the narrow range of 0.05–0.09 m./sec. The averaged origins are found to be restricted to the region of one electrode about 2 mm. posterior to the tip of the posterior ectosylvian sulcus; the averaged entry zone is found to lie about 2 mm. below and anterior to the average origin. Interpreting these findings liberally, the average traveling edge originates in a band just behind the upper end of the posterior ectosylvian sulcus, and travels across the array at a relatively constant velocity in all directions from this band.

However, if the calculations are restricted to the first 78 msec. of each figure, the plotted results show the same band of origin, but a new zone of entry appears posteriorly (Fig. 2). The traveling edges from these two averaged areas strike each other at about 26 msec. This latter fact does not necessarily mean that there are two figures simultaneously present on the cortex: the averaged picture includes figures coming from each zone at different, widely separated zero times (Methods); in no case were two such figures seen in the array at the same time (6: Figs. 8, 9). The movements of the figures in the anterior part of the active area are a bit faster than in the first case; the figures in the posterior zone are speeded up by a factor of 3 to 4 times: however, as will be shown later, there are too few figures entering posteriorly to give an accurate estimate of this average velocity.

Trailing edge. As in the first case of the averaged leading edge (Fig. 1),

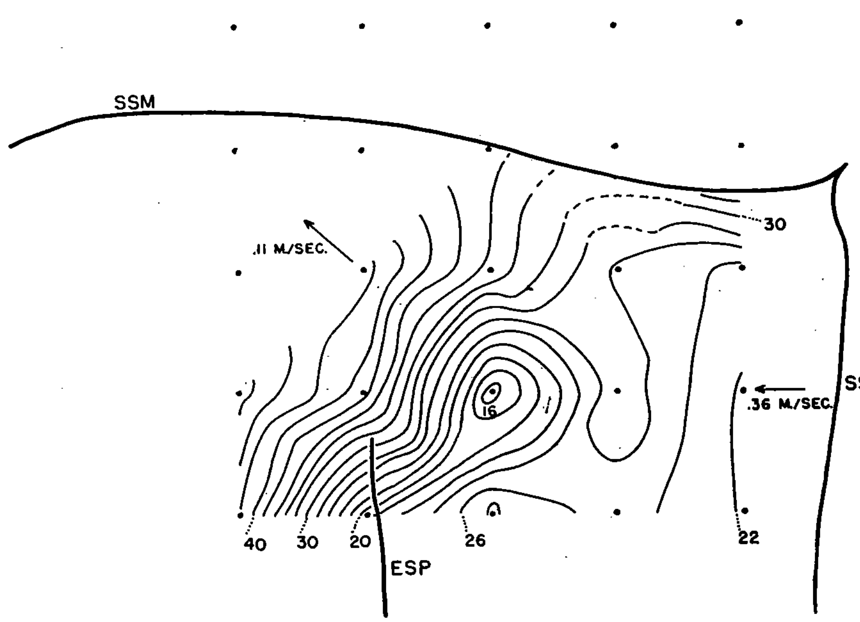

FIG. 2. *Sequential positions of averaged leading edges for first 78 msec. of each figure.* In contrast to preceding map (Fig. 1), average positions of leading edge are taken for only first 78 msec. of each figure; this procedure avoids overlap of courses of figures of preceding chart. Anterior origin remains in same place as before but occurs earlier (16 msec. and 20 msec.). A new origin appears in posterior edge of array near SSP; entering velocity (0.36 m./sec.) of figures from this region is higher than in those from anterior origin (about 0.1 m./sec.). Due to fact that only a few figures start in posterior origin (Fig. 5), previous chart showed mostly velocity of travel (0.09 m./sec.) in this posterior region of figures starting in anterior origin. As they enter, figures entering posteriorly have highest velocity (0.36 m./sec.) found for any of these figures.

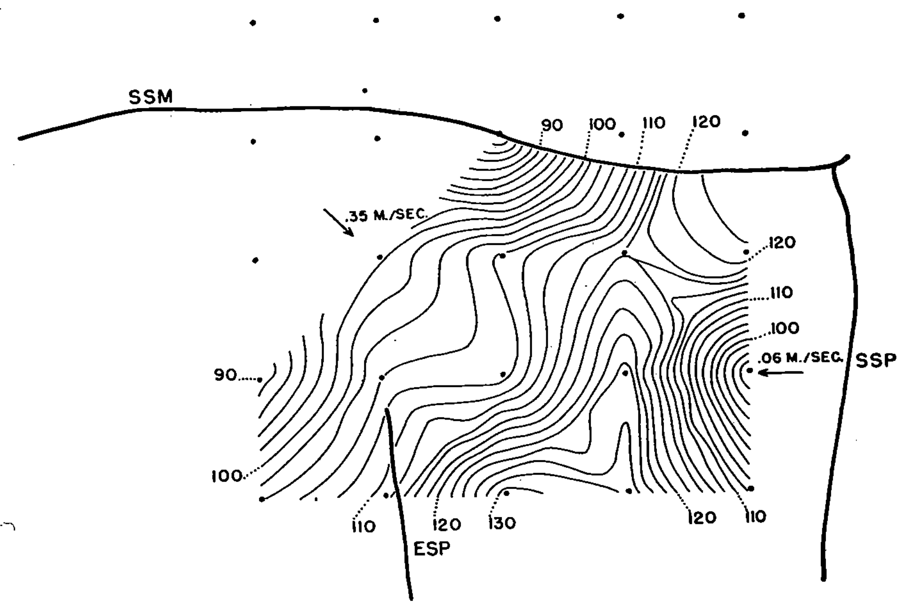

FIG. 3. *Averaged sequential positions of trailing edge.* Highest velocity for trailing edge (0.35 m./sec.) is in region of lowest velocity (0.05 m./sec.) for leading edge (Fig. 1); lowest velocity (0.06 m./sec.) is in region of highest velocity (0.26 m./sec.) for leading edge (Fig. 2). General direction of movement for trailing edge is toward center and downward.

the averaged trailing edge includes all cases of activity which end at each electrode (Fig. 3). The general direction of movement is downward toward the lower limit of the array. (There is one doubtful exception in the upper right hand corner of the active region where there are too few electrodes and observations to be certain.) The velocities range from 0.06 m./sec. to 0.35 m./sec. in the indicated regions and directions; this velocity range overlaps that of the first leading edge (0.05 to something over 0.09 m./sec., Fig. 1) and that of the second leading edge (0.11–0.36 m./sec., Fig. 2). The region of the fastest trailing edge (0.35 m./sec.) corresponds to the region of the slowest leading edge (0.05 m./sec., Fig. 1); this region, above and behind the upper end of the posterior ectosylvian sulcus, was shown to be the region of the convergence and termination of the slow leading edge (0.06–0.19 m./sec.) of the click responses (7: Fig. 1), and is just above the region of the most frequent origins of the spontaneous figures (see below). The region of the slowest trailing edge (0.06 m./sec.) is the region of the fastest leading edge (0.36 m./sec., Fig. 2), and lies near the posterior zone of entry for the figures. In each of the above cases, the direction of the fast movement is at about 180° to the slow one, and the ratio of the largest to the smallest speed is about 6 or 7 to 1 in each region.

Durations of activity. The averaged durations of activity at each cortical point are found to give a rather symmetrical picture (Fig. 4) when compared to irregular ones for the leading (Fig. 1) and the trailing (Fig. 3) edges from which they are derived; the shortest durations are around the right hand, left hand, and upper periphery, and the longest, at the lower center part of the active region; the rate of change of duration with respect to distance across the cortex has two relatively constant values, one around the periphery (about 23 msec./mm.) and the other in a central part of the active area (about 5–10 msec./mm.). The central part, which has the smaller duration gradient, lies just behind the anterior, most frequent origin of the figures and ahead of the posterior, less frequent, zone of entry (Figs. 1, 2). In other words, the figures tend to last longer in this central part than in the peripheral parts, and in general this tendency has a gradient in from the periphery and downwards along the cortex.

Variability. The averaged leading and trailing edges and durations are for the whole population of 20 spontaneous figures. The variability of the behavior of the various individuals within the population is shown in charts plotting the fraction of the population at each cortical point which (a) have a leading edge reaching that point first (Fig. 5), (b) have a trailing edge leaving that point last (Fig. 6), and (c) include the point in their maximum extent (Fig. 7).

The number of individual figures which have a leading edge which reaches given cortical points first (Fig. 5) is a maximum in the region of the anterior origin of the leading edge (cf. Figs. 1, 2, 5): the line for 0.4 of the

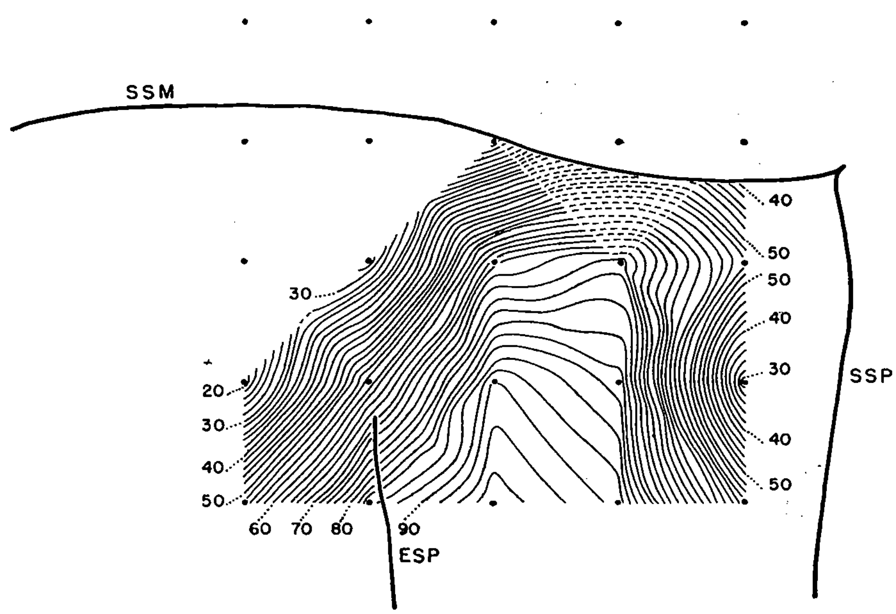

FIG. 4. *Distribution of durations of activity.* Duration at each point is elapsed time between leading edge (Fig. 1) and trailing edge (Fig. 3) at that point. Shortest durations (30 msec.) are around periphery, the longest (96 msec.) near center and bottom of array. Minimum rate of change of duration with cortical distance (5–10 msec./mm.) occurs in central part, and maximum rate (23 msec./mm.) occurs around periphery.

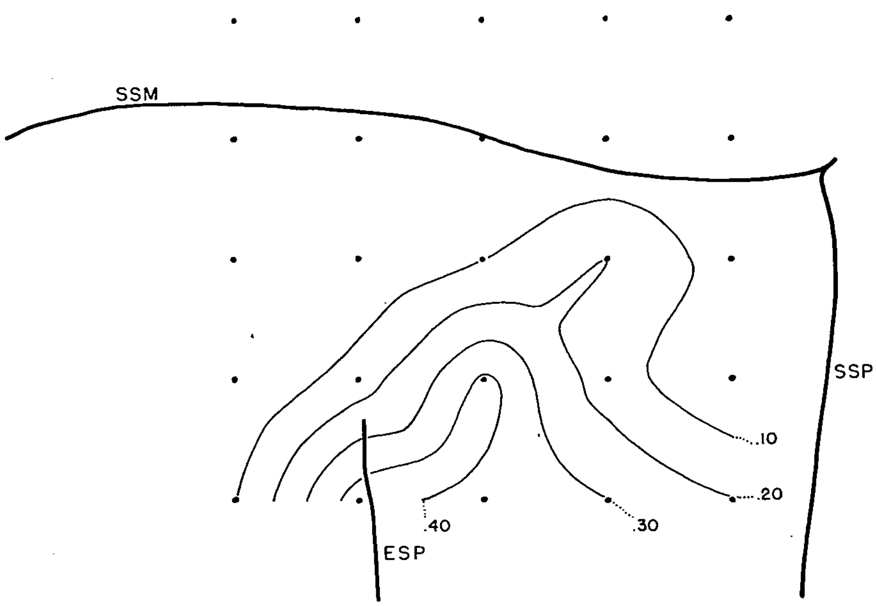

FIG. 5. *Positions first reached by leading edge.* Numbers refer to fraction of total number of figures whose leading edge entered given area first. Most of figures (40 per cent) enter in anterior origin; very few (10–20 per cent) enter in posterior region of entry (Figs. 1, 2). Gradient of first entry is uniformly about two figures per mm. and is directed away from anterior origin.

total individuals surrounds this origin and entry region. The fraction of the total individuals drops off fairly uniformly with distance from this zone of the maximum fraction at a rate of approximately 0.1/mm. of cortex, or two individuals per mm. The region of the posterior entry of figures into the array (Fig. 2) contains the 0.1 and 0.2 fraction lines; relatively few individuals entered the array here. An inspection of the individuals of the population (6: Figs. 8, 9) shows that seven of the 20 individuals started at one or more electrodes completely within the array; the other 13 appeared first at electrodes at the array's periphery.

The number of individual figures whose trailing edge leaves given cortical points last is a maximum along the lower edge of the array in the posterior ectosylvian gyrus (Fig. 6); the average gradient of this number varies from 1 to 2.5 individuals per mm. and is directed predominantly downwards on the cortex. Only two of the 20 individuals ended on electrodes wholly within the array (6: Figs. 8, 9). These results reflect the tendency of the figures to move downward on the gyrus (Fig. 3).

The number of individual figures which touch upon a given set of cortical points during the time of the maximum extent (within the array) of each figure is at a maximum in a central zone of the active region (Fig. 7); the gradient of this number is within the range of four to eight individuals per mm., and is directed uniformly away from the central peak zone within the array. This central zone includes the region of the anterior origin of the figures (Figs. 1, 2) and the region of the maximum durations of the figures (Fig. 4): 90 per cent (or 18) of the 20 figures shared this region at the time of their greatest area included within the array. An analysis of the areas of the individual figures (6: Figs. 8, 9) was made assuming each active electrode, on the average, represents the activity of 4 sq. mm. of active cortex. The average maximum area of the figures is 26 sq. mm., with a minimum of 20 and a maximum of 32 sq. mm. for the extreme individuals (four high and four low). This average maximum area represents approximately the active area assigned to six electrodes; there are six electrodes which include 90 per cent of the individuals at their maximum extent (the 0.90 line, Fig. 7); it is concluded that the 90 per cent central zone most frequently represents the region in which the average figure at its maximum extent tends to occur; this central zone does not represent as frequently an area of overlap for the maximum extent of a group of figures each of which is either much smaller or much larger than the central 90 per cent zone.

Relations to acoustic stimuli. In addition to the above data, from other records at about the same anesthetic level it was found that there are certain relations between these spontaneous figures and acoustic stimuli (clicks in trains at a rate of 1/sec. and loud noises). As has been shown previously (6, 7), the click response occurs in an area just anterior to and overlapping with the forward part of the area showing spontaneous activity (Figs. 1–6).

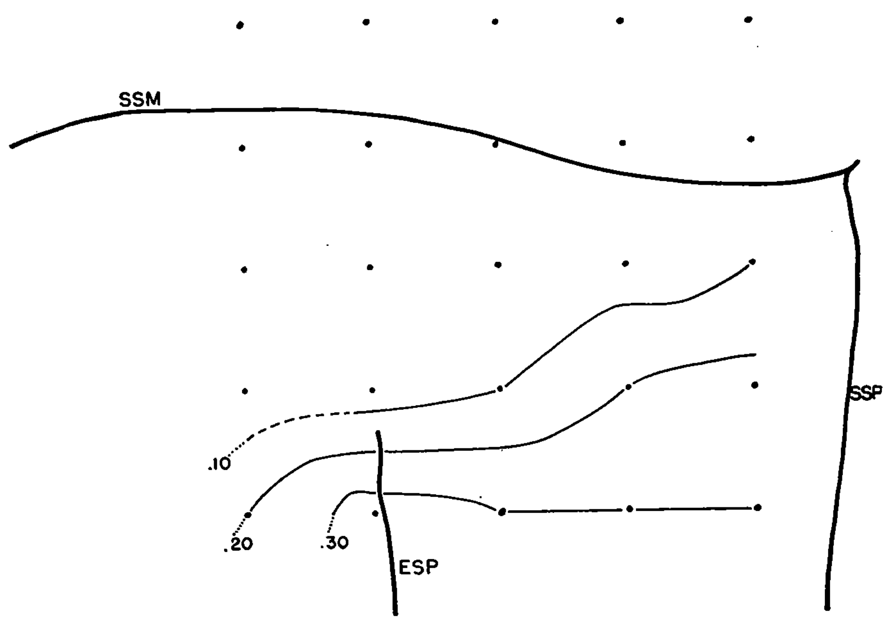

FIG. 6. *Positions last left by trailing edge.* Numbers refer to fraction of total number of figures whose trailing edge dies away at or leaves each point last. Maximum fraction is along lower border of array. Gradient is directed away from this border and is from 1 to 2.5 figures per mm.

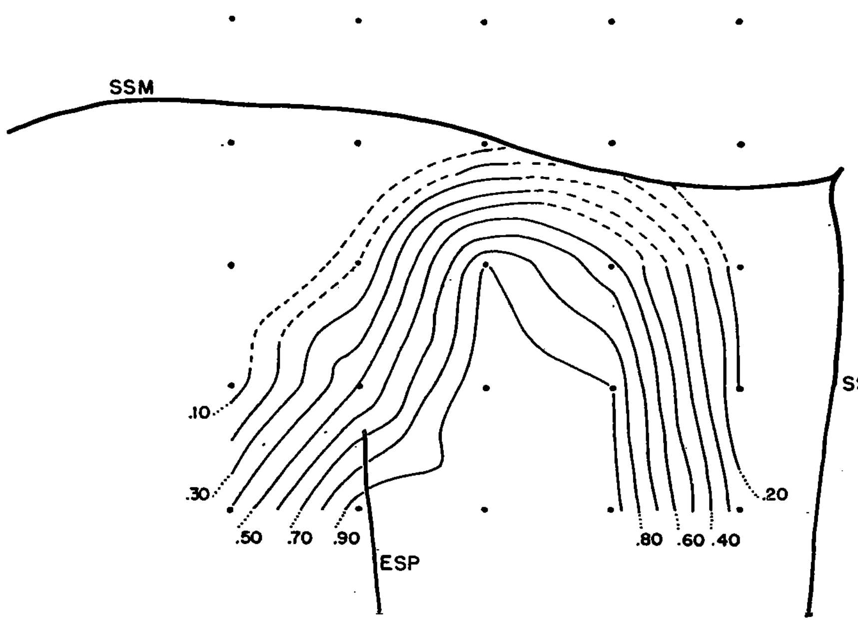

FIG. 7. *Positions occupied by figures at maximum extent.* Numbers express fraction of figures whose edge, at the time of its maximum included area of extent, contained each cortical point. Maximum number of figures (90 per cent) occurred in central part of active area. Gradient is directed fairly uniformly away around this area and is four to eight figures per mm. The 90 per cent line includes an area corresponding to average area at maximum extent of total number of figures (text).

If, during a train of clicks and their responses occurring at a rate of 1/sec., spontaneous figures occur, the origin of the spontaneous figure shifts with time after the click: during about the first 500 msec. the origin is always the anterior one near the response area; later than 500 msec. the figures originate in the posterior zone whether or not there was a previous figure from the anterior zone. After each figure started to grow, it moved into the area of maximum extent (Fig. 7) and appeared to be the same at this phase irrespective of its origin, in a fashion similar to the above figures occurring without click stimuli.

If, instead of clicks, a sharp loud whistle or any sharp loud noise is made after a long period of quiet, a large response is seen in the response area (7) and after the response has reached its peak, a figure very much like the spontaneous ones originates in and starts moving posteriorly out of the anterior origin (Fig. 2); after they are moving, such figures are indistinguishable from the spontaneous ones. This elicitation of such figures cannot be repeated oftener than once about every 5–15 sec. despite the fact that the response area can be made to show activity as often as once per sec. The latency of the figure arising in the anterior origin (Fig. 2) is difficult to determine accurately: its value is approximately 100 msec. after the start of the response in the response area. To elicit such a figure there must be a long period (5–

15 sec.) of low or no activity in the whole acoustic system and then a relatively long period (50 msec. or more) of intense activity in the acoustic system.

Discussion

An electrical figure is defined as a pattern of variation of electrical potential which at a given instant has a closed set of equipotential surfaces in three dimensions in the brain and its immediate surroundings, and which may change with time in size and/or in location (6). Such figures are assumed to be the electrical signs of figures existing in the activity of circumscribed populations of neurons and their processes; the changes in size and in location of the electrical figures reflect the changes in the participating populations of active cells and processes. Presumably, the electrical figures can have sizes and time relations which vary with the size and spacing of the electrodes in the array used to view them: 0.5 μ diameter microelectrodes placed 2 μ apart might give part of the rapid electrical figure of a single cell body or of part of the processes of one or of many neurons; at larger spacings, the array of microelectrodes may show activity not identifiable as a continuous and connected pattern, or may show figures dotted by spots of intense activity related in unknown ways to the figures. Thus it can be seen that the figures described in this and the preceding papers (6, 7) are characteristic for the size, spacing, number of the electrodes, and the area of the array. How much the appearance and character of the figures depend on these variables can be shown only with other arrays in the future. Presumably, the relatively large figures analyzed here contain smaller figures and also are parts of larger figures in large zones of the brain.

In this paper certain spontaneous electrical figures in the posterior ectosylvian gyrus are examined in regard to their origins, growth, movement, and die-away patterns. Two origins or zones of entry into the array are found, an anterior one near the click response area and a posterior one near the posterior suprasylvian sulcus (Fig. 2). In a state of relative quiet in the environment and at a suitable, constant level of anesthesia, these figures occur spontaneously about once per sec. The anterior origin is the most frequent source (Fig. 5), is the only source for spontaneous figures for about 500 msec. after a click in a train at a rate of 1/sec., and is the source of similar figures which follow an intense, long acoustic stimulus. The posterior origin is preferred as a source infrequently in the quiet environment and most frequently after the first 500 msec. after each click in a train of clicks occurring at 1/sec. After each figure is started certain aspects of the figure's growth and travel pattern are shared with the other figures of the group: the area of maximum extent tends to be centered in the posterior ectosylvian gyrus (Figs. 4, 7), the predominant direction of movement is downward along the gyrus (Figs. 3, 6), and the speed range is from 0.05 to 0.36 m./sec.

The cytoarchitectonics of the posterior ectosylvian region and of the area giving responses are described by Rose (11); he gives a boundary between the two regions just posterior to the posterior ectosylvian sulcus and just posterior to a line extending from the upper end of this sulcus to the middle suprasylvian sulcus. This boundary is between acoustic I (AI) and his posterior ectosylvian field (Ep). His posterior ectosylvian field takes up the middle of the posterior ectosylvian gyrus, extends upward to the middle surprasylvian sulcus, and extends to a line just anterior to the posterior ectosylvian sulcus (11: Fig. 1). In contrast to the medial geniculate projection to acoustic I, definite subcortical projections are not found for the posterior ectosylvian region (12). In the young cat, the posterior ectosylvian region receives myelinated fibers at 10 days after birth, after acoustic I and before the temporal cortex lying more ventrally (11). The cytoarchitectonics and the myelinization history establish the posterior ectosylvian region as a single cortical field in the anatomical sense. The data of the present paper indicate that this field also has a very characteristic spontaneous activity which ultimately may be explained by the structure of this cortex and its connections. So far, only the following suggestions can be offered in regard to correlations between structure and activity.

Assuming for discussion purposes that the cortex contains 40,000 cells per cubic mm., at a given instant a given electrical figure of the type analyzed here (whose maximum area may be between 20 and 32 sq. mm.) lies in a region containing (in a slab of cortex 1 mm. thick) a total of between about 800,000 to about 1,280,000 cells. As will be shown in the next paper of this group, the peak potential difference across the figure and its surroundings is about 500 μV. in the surface-positive direction. Presumably, all of these cells are not necessarily synchronously active at this instant; if they were so active, the peak potential difference would be 100 times the 500 μV. peak found, as is found for the spike elicited by placing strychnine on the cortex. Another possibility is that only a small fraction of the cells are synchronously active, and that the electrodes are picking up activity in their processes in the superficial cortical layer; however, this is unlikely. Adrian's (1) and Burns' (2) results show only surface-negative responses to stimulating only the processes in the superficial layer of the cortex; when a surface-positive response was elicited, apparently deeper cell layers were stimulated. It is concluded that these predominantly surface-positive figures are due to activity in some at present unknown system of deep cortical cells and their processes. Since the figures have closed boundaries which enlarge with time, there are presumably rich interconnections between these cells (and their processes) in directions parallel to the cortical surface. The slow speeds of growth, travel, and die-away; the long durations of activity at each point; the large size of the active area at each instant; and the invasive directions of new growth, are all consistent with the view that the electrical figures are generated by a cell system which has short, multisynaptic, and numerous interconnections in each small area. Part of the picture may be due to the slow travel of activity in small and numerous cell processes, but the high value of relatively surface-positive potential (500 μV.) at the center of the figure suggests that the main activity is that of a closely packed, synchronously active, deep cell population.

The general tendency of the spontaneous figures to move downward along the gyrus (Figs. 3, 6) may be related to the "cytoarchitectonic field" gradient found by Rose (11) in the dorso-ventral direction; of course, this direction of movement may also be determined by at present unknown subcortical connections and movement of figures in other nuclei. The general velocity of movement is not inconsistent with a strictly cortical determination of this velocity: the velocities found by Adrian (1) in intact cortex electrically stimulated (0.1–0.4 m./sec.) and by Burns (2) in isolated cortex similarly stimulated are of the same order as our extreme range (0.05–0.36 m./sec.) for both the leading and the trailing edges; in addition, the way each figure grows from its initial small origin looks like a purely cortical growth and travel but is later confined as it reaches a boundary of changed structure (between Ep and upper AI); but this growth could as easily be one occurring concomitantly both in cortex and in certain subcortical nuclei, either with or without feedback (7). There is not enough evidence at present to decide between these alternatives.

The observations on the two separate origins for the figures suggest that there are at least two subcortical systems which can initiate these figures: what or where they are is not known. A rather intriguing possibility which we present as a tentative suggestion is that the anterior origin is a focus of important connections with the reticular activating system (14) and the posterior one has important connections with the recruiting response system (5, 8, 13, 15).

The anterior origin of the figures (Fig. 2) can be excited to produce a figure by means of an intense, prolonged sound not repeated oftener than once every 5–15 sec.; this figure, of course, can be due to intracortical activity transmitted across the AI-Ep boundary with or without concurrent activity started by collaterals to "non-acoustic" nuclei. This origin is conditioned in such a way as to favor it as a preferred source for a figure for 500 msec. after a click. It is suggested that this origin is a dominant focus of projections from the reticular activating system (3, 14), which is excited by loud noises and, presumably, is conditioned by click stimuli (10); also, the anterior origin may have a projection back to this reticular system which would be active whenever the anterior origin is active.

The posterior origin, near the posterior suprasylvian sulcus (Fig. 2), lies close to an area which is reported to be a dominant focus in the cortex for the recruiting response elicited from the thalamus by Starzl *et al.* (14); their posterior suprasylvian focus is pictured as just reaching the posterior ectosylvian gyrus in a region approximating our posterior origin for spontaneous figures; Rose (11) shows that this region is not the type of cortex belonging to the posterior ectosylvian field but belongs to that of the posterior suprasylvian gyrus. In the original map of the loci for maximal recruiting response of Morison and Dempsey (8), there is a suprasylvian focus but it is not shown crossing the sulcus; in the map of Hanbery and Jasper (5) dominant foci are not pictured and the upper part of the posterior ectosylvian field is included in the areas showing the recruiting response. A possible explanation of the results of Hanbery and Jasper in this posterior ectosylvian field is that they stimulated the thalamic system under the proper conditions so that one of the figures was started in the posterior origin and moved into the ectosylvian field, giving the response shown (5: Fig. 4). In a later paper, it is shown by us that a similar "cortical" growth and subsequent travel of spontaneous figures can occur in acoustic II from figures fully developed in the posterior ectosylvian field; the ones elicited in acoustic II have a higher velocity than in Ep; these observations may explain the finding of responses in A II by Hanbery and Jasper (5) where they were not found frequently by Morison and Dempsey (8), and rarely if at all by Starzl and Magoun (13). Hanbery and Jasper may have had the anesthesia, the location and the intensity of the stimulus just right to stimulate figures of the type presented above; the other authors may have been using deeper anesthesia, slightly different stimulated zones, and/or a weaker stimulus, thus avoiding the elicitation of the traveling figures.

There seems to be a relation between a certain type of spontaneous activity found "throughout the hemisphere" (including the posterior ectosylvian field), the secondary response to peripheral nerve stimulation (3, 4, 9) and the spontaneous figures in this paper. Morison *et al.* (9) show that single spontaneous waves and the secondary response can occur with all connections to the hemisphere cut except for a small bit of white matter near the temporal horn of the lateral ventricle; their records show large single slow waves in the posterior ectosylvian gyrus (9: Fig. 2, p. 746). The secondary response may be due to stimulation by collaterals of the reticular activating system (14); hence, the single spontaneous waves using the same fiber tracts may originate in this system. Presumably, the single waves, spontaneous or evoked, represent a figure like the ones presented above, as recorded by a single electrode; with a single electrode, the place of origin would not be distinguishable. In line with our above suggestions, the anterior origin would be the one most likely to give rise to the single spontaneous waves and to the secondary response.

We wish to emphasize that such a new way of looking at spontaneous activity as we have presented here may generate more of the uniqueness of our findings in the posterior ectosylvian gyrus than the gyrus itself possesses; there may be other, fairly large areas of the cat cortex which possess similar activities. However, some of our unpublished results on the visual cortex of the cat show quite different spontaneous figures which are long and narrow traveling bands of activity instead of the round, circumscribed figures analyzed here. A previous paper (7) shows that the same method applied to responses in a primary projection area gives an entirely different picture in that area. The generality of these two pictures, one in "association" cortex and one in "projection" cortex, is yet to be determined.

Summary

A group of 20 figures appearing in the electrical spontaneous activity of the posterior ectosylvian gyrus of a cat at a certain level of nembutal-dial anesthesia was recorded with an array of 25 electrodes simultaneously. The records were analyzed for the times of occurrence of the sequential positions on the cortex of the beginnings ("leading edge") and the endings ("trailing edge") of the activity at each cortical point as each figure traveled across the array. The figures occurred in a period of about 25 sec. at an average rate of about one figure per sec.; each figure is a single entity; at one electrode the associated waveform is a single, slow, predominantly surface-positive deflection (6). This type of activity is characteristic of the posterior ectosylvian region at this level of anesthesia.

The positions and times of occurrence of the leading edges of all 20 figures were averaged over the whole time of occurrence (Fig. 1) and over the first 78 msec. of each figure (Fig. 2). These results show that there are at least two originating zones for the figures: one near the upper end of the posterior ectosylvian sulcus (the anterior origin) and one near or in the posterior suprasylvian sulcus (the posterior origin). The extreme speeds of travel of the edges of the figures fell within the range 0.05–0.36 m./sec., in directions away from the origins.

The average trailing edge (Fig. 3) moved predominantly toward the center and bottom of the active region at speeds within the range of those of the leading edge.

The average elapsed time between the arrival of the leading edge and the departure of the trailing edge at each cortical point was calculated and mapped (Fig. 4); there is a central zone with a small gradient of duration and a peripheral zone with a large rate of change. The zone of the smaller gradient corresponds to that in which 90 per cent of the figures are contained at the time of their maximum extent (Fig. 7).

The map of the number of figures whose leading edge first arrived at a given cortical point (Fig. 5) shows a maximum around the anterior origin. A chart of the number of figures whose trailing edge last departed from a given cortical point (Fig. 6) shows a maximum at the lower border of the array. A map of the number of figures whose area at the time of maximum extent included a given cortical point (Fig. 7) shows a maximum in the central part of the active region which includes the anterior origin.

From these charts, the behavior of the average spontaneous figure is as follows: (a) it originates either in an anterior origin (most frequently) near the dorsal tip of the posterior ectosylvian sulcus or a posterior one near or in the posterior suprasylvian sulcus; (b) it grows as it moves from the origin toward the center of the upper part of the posterior ectosylvian gyrus (two small figures died before growing); (c) it takes up its maximum included area as it reaches this center; (d) it then moves dorso-ventrally along the center of the gyrus to the lower part of the gyrus.

Similar figures can be elicited at the anterior origin by intense, relative-

ly long sounds; trains of clicks so condition the mechanisms generating the spontaneous figures that figures occur only at the anterior origin for the first 500 msec. after click and at the posterior origin for the second 500 msec.

All speeds found are in a range similar to that of the cortical surface-positive response of Adrian in intact cortex (1) and of Burns in isolated cortex (2). A suggestion is made that the anterior origin is connected with the reticular activating system, and the posterior one with the recruiting response system.

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