ELECTROENCEPHALOGRAPHIC PHASE REVERSAL
OBSERVED IN CHICKENS

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OOKAWA and GOTOH8,9,10) have studied the surface electroencephalogram (EEG) of chickens by the chronic experimental method and determined its normal patterns from wakefulness to sleeping and the effect of anesthesia on EEG.

In their experiments, electric activity revealed many interesting characters, including phase reversals at certain regions of the brain.

The phase reversal mentioned above, was originally observed in the examination of a series of leads on the surface of the skull, including the frontal and parietal regions, for relative polarity.

Owing to the dipole hypothesis concerning the EEG origination, it was suggested from this examination that further attempts might possibly determine the site and role of the dipole as the origin of EEG.

In the present experiment, analysis was made on the electric field concerning the phase reversal by using the bipolar leads of chronically implanted electrodes.

METHODS

White Leghorn roosters about 3 months of age weighing 1.5 to 2.0 kg were used. Electroencephalograms were recorded by an 8-channel EEG apparatus with silver ball electrodes 1 mm in diameter (over-all time constant: 30 msec.). These electrodes were implanted upon the dura mater and settled on the skull with dental cement or self-curing acrylic resin. The electrodes were fixed unilaterally to the frontal and parietal bones in such a manner as shown in Fig. 1. The inner electrodes were placed 3 mm and the outer ones 6 mm lateral to the median line. The points planted on the skull were 3 mm apart both longitudinally and transversely.

The electrode implantation was performed under pentobarbital (Nembutal used) anesthesia (30 mg per kg of body weight injected intravenously or intraperitoneally). An EEG was recorded for the first time at least 24 hours after the electrode implantation. All records were obtained under restrained conditions. The room temperature was maintained at 18 to 22°C during the period of recording. The other procedures for the preparation of EEG's were the same as described in the previous report.

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RESULTS

Four unanesthetized chickens (Nos. 215, 219, 220, and 221) presented the following EEG patterns against a series of waves led from the electrodes located on a longitudinal line 3 mm lateral to the median line of the brain.

In three chickens, Nos. 219, 220, and 221, waves with a slow frequency of 2 cps were predominant. The amplitude of these waves on the surface negative at a lead between electrode positions P. 1 and P. 2 (Le. 1-2) was 10 $\mu$V, and that at Le. 2-3 zero. Then the amplitude increased to 15 and 30 $\mu$V at Le. 3-4 and Le. 4-5, respectively, with a surface positive deflection, the frequency of which was also 2-3 cps. It is of great interest to note that in the course of recording, the leads showed a sudden decrease in amplitude at Le. 2-3 and the reversed polarity appeared at Le. 3-4 and Le. 4-5. On the other hand, each of the subsequent waves led from Le. 3-4 or Le. 4-5 increased more and more in amplitude as the lead was shifted toward the posterior position. The leads producing an increasing voltage were arranged in the following order: Le. 2-3 and Le. 1-2 in the negativity, and Le. 3-4 and Le. 4-5 in the positivity. Thus polarity reversal, or phase reversal, was observed between Le. 1-2 and Le. 3-4 (Fig. 2).

Furthermore, in a series of leads derived from such electrode positions as on a longitudinal line 6 mm lateral to the median line, the same phenomena as described above were observed. In this case, the amplitude of the most frontal lead, Le. 6-7, was 20 $\mu$V, the frequency of which was 2-3 cps. The amplitude of Le. 7-8, Le. 8-9, and Le. 9-10 was 10, 35, and 35 $\mu$V, respectively. The phase reversal was observed between Le. 8-9 and Le. 9-10, as shown in Fig. 3.

Two chickens, Nos. 216 and 217, were used to obtain results under pentobarbital anesthesia which had been induced by a dose of 30 mg per kg of body weight injected intravenously.

In the case of chicken No. 216, a spike and slow wave with an amplitude of 100 $\mu$V at 1-3 cps, was observed distinctly at Le. 8'-9' and Le. 9'-10', and the
FIG. 2. EEG recorded from intact chicken No. 220. Phase reversal is shown between Le. 1-2 and Le. 3-4.

FIG. 3. EEG recorded from intact chicken No. 219. Phase reversal is shown either between Le. 1-2 or Le. 3-4, and between Le. 8-9 and Le. 9-10.
polarity reversed apparently between Le. 1'-2' and Le. 3'-4', between Le. 6'-7' and Le. 7'-8', and between Le. 7'-8' and Le. 8'-9' (FIG. 4). In the other bird, No. 217, however, there was not a spike, but a sole sharp wave with an amplitude of 20-50μV and 2-4 cps at every lead, and the phase reversal was shown apparently between Le. 1'-2' and Le. 3'-4' and between Le. 6'-7' and Le. 7'-8' (FIG. 5). Electrode positions P.1' to P.10' were 1.5 mm posterior to standard positions P.1 to P.10, respectively.

These results clearly indicate that both unanesthetized and anesthetized chickens presented significant phase reversal between Le. 1-2 and Le. 3-4, or Le. 1'-2' and Le. 3'-4'. The unanesthetized chickens revealed another phase reversal between Le. 8-9 and Le. 9-10, and the anesthetized chickens did between Le. 6'-7' and Le. 7'-8'.

FIG. 6 shows the relationship between the measured voltage of waves with a peak amplitude of the slow waves (2-3 cps) and the leading point. These results have made it clear both in unanesthetized and in anesthetized chickens that in a series of leads located on a longitudinal line 3 mm lateral to the median line, the voltage led from a posterior position, i.e., Le. 4-5 and Le. 3-4, or Le. 4'-5' and Le. 3'-4', decreased more and more as the lead was shifted from
FIG. 5. EEG recorded from chicken No. 217 under pentobarbital anesthesia. Phase reversal is shown between Le. 1'-2' and Le. 3'-4', and between Le. 6'-7' and Le. 7'-8'.

No. 215: No. 219: No. 216: No. 221: No. 217:

FIG. 6. Relationship between the measured voltage of waves with a peak amplitude of the slow waves (2-3 cps) and the leading point. The vertical lines 1-10 indicate the points where electrodes were implanted, and the horizontal ones voltage of peak amplitudes.
the dorsal to the frontal region, and that the decreased voltage was followed by a suddenly increased one (Le. 1-2 or Le. 1'-2'). In other words, the voltage was the lowest at Le. 2-3 and higher either at the frontal (Le. 1-2 or Le. 1'-2') or at the dorsal lead (Le. 3-4, Le. 4-5, Le. 3'-4', or Le. 4'-5'). At that time, phase reversal occurred at the position of the lowest voltage, i.e., between Le. 1-2 and Le. 3-4 or between Le. 1'-2' and Le. 3'-4'. Thus the dipole seemed to be present at electrode position P. 2, or 1.5 mm posterior to that position.

On the other hand, in a series of leads fixed on a line 6 mm lateral to the median line, higher voltage tended to appear at a posterior lead, Le. 8-9, 9-10, 8'-9', or 9'-10', and lower voltage at a frontal lead, Le. 7-8, 6-7, 7'-8', or 6'-7', both in anesthetized and unanesthetized chickens. In other words, the voltage decreased gradually as the lead was shifted from dorsal to frontal. In this case, phase reversal appeared between Le. 8-9 and Le. 9-10 or between Le. 6'-7' and Le. 7'-8'. Thus one dipole in unanesthetized chickens existed under electrode position P. 9, where higher voltage was distributed, and the other dipole in anesthetized chickens under those positions where somewhat lower voltage was distributed (P. 7'). Thus, the dipole in the anesthetized chickens was 4.5 mm more frontal to that in the intact chickens.

**DISCUSSION**

WALTER[14] (1949) and BRAZIER[2] (1953) believed that the EEG was the results of summation of activities projected from dipoles subcortically oriented. WALTER demonstrated in human beings that the potential field of the skull upon the cerebrum had the same properties as shown in a model consisting of a spherical volume conductor and its internal dipole. On the basis of her hypothesis, BRAZIER analyzed the electric field upon the surface of the skull and concluded that the alteration in the orientation of an electrode to the skull induced changes in potential distribution.

In addition to WALTER and BRAZIER, many investigators, such as ECCLES[3], BREMER[4], COOPER[5], LINDSLEY[6], and PANTEK[11] established different theories concerning the origin of EEG.

TOWE and RUCH[13] (1961), however, pointed out as follows. Several lines of evidence show that the EEG in mammals depends for its existence upon the electric properties of cortical cells, especially the pyramidal cells. Certain characteristics of the essential processes can be surmised from the basic properties of individual cells. The electrical space-constant of the cell body is so large that the cell body must behave as a unit, i.e., show no dipole properties. On the other hand, the minute dendritic projections of the soma, because of their high internal resistance, have space constants less than their own length. This means that they should be seen as moving dipoles by a distant electrode immersed in the same volume conductor. It is for this reason that many believe
the EEG to result from the summation of dendritic activity and especially of any vertically oriented projection, which should be, on the average, closer to a surface electrode and show a greater solid angle.

Recently Rosenthal et al. \((1966)\) reported that the soma of the pyramidal cells in the cerebral cortex of cats had dipole properties, from which he proposed the following formula:

\[
V = K \frac{1 + \gamma S}{(1 + S^2)^{3/2}}
\]

where \(V\) was a dipole represented by the vector, \(\gamma = \tan \theta, \theta\) was the angle between a dipole and the distance to the point on the electrode track \((R_0)\), and \(S = s/R_0, s\) was the distance from the point of the closest approach to the dipole.

In the present experiment, phase reversal was observed between Le. 1-2 and Le. 3-4, Le. 1'-2' and Le. 3'-4', Le. 8-9 and Le. 9-10, and Le. 6'-7' and Le. 7'-8'. So two principal dipoles might be present in the striatum. One of them might exist under electrode position P. 2 or a point 1.5 mm frontal to P. 2 (P. 2'), and the other one under P. 9 or 4.5 mm frontal to P. 9 (P. 7'). According to Rosenthal's \((1966)\) report the axes of the former dipole seemed to be parallel to the surface of the skull, while that of the latter vertical. In chickens no pyramidal cell-layer has been found in any region of the surface of the brain.

In the region ventral to electrode positions P. 2, P. 2', P. 9, and P. 7' lies an area named ectostriatum by Huber and Crosby \((1929)\).

Recently Kito \((1967)\) observed the presence of specific cell groups composed of large cells, 16-19\(\mu\) in length and 7-10\(\mu\) in width, medium sized cells, 11-16\(\mu\) in length and 7-10\(\mu\) in width, and small cells, 10\(\mu\) in length and 6-7\(\mu\) in width. These cell groups were distributed especially in the ectostriatum, which the authors suggested as the site of dipoles.

Whether the specific cells observed by Kito act as dipoles or not should be studied in a further experiment.

No satisfactory explanation has been made for the result that the focus of phase reversal observed on a line 6 mm lateral to the median line in anesthetized chickens was different from that in unanesthetized ones.

**SUMMARY**

1. By using the linked method, the electric field of the chicken brain was observed under restrained conditions to determine the presence of a dipole.

2. One of the two foci of phase reversal observed was between Le. 1-2 and Le. 3-4, or between Le. 1'-2' and Le. 3'-4', and the other was between Le. 8-9 and Le. 9-10, or between Le. 6'-7' and Le. 7'-8', both in unanesthetized and anesthetized chickens.

3. According to the dipole hypothesis concerning the origin of the electro-
encephalogram, one dipole was present under these foci of phase reversal, or at electrode position P. 2 or P. 2 : 9 or 7.5 mm frontal to the bregma and 3 mm lateral to the median line, and the other one at electrode position P. 9 : 3 mm frontal to the bregma and 6 mm lateral to the median line.

4. In anesthetized chickens, however, a dipole seemed to be present under electrode position P. 7 : 7.5 mm frontal to the bregma and 6 mm lateral to the median line.

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