Developmental EEG of the Beagle Dog

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ABSTRACT. The developmental electroencephalogram (EEG) was recorded from 64 beagles to make a map on the normal EEG in relation to the change of age and the state of consciousness, and to establish the criterion of evaluation on the abnormal EEG. Montages used were four rhinal reference recordings (LF-R, RF-R, LO-R, RO-R) and four bipolar ones (LF-RF, LO-RO, LF-LO, RF-RO). Rhythmic waves which were occasionally seen at the 1st postnatal day increased with days of age and appeared constantly in the 7th postnatal day. The wakefulness and sleep were distinguished in the EEG of two weeks of age. It was revealed that the EEG on the 5th week could be classified into wakefulness, light sleep, middle sleep and deep sleep, because prototypes of all wave patterns or wave forms such as desynchronizations, rhythmic waves of 8–13 Hz, humps, primitive spindles and slow waves below 3 Hz occurred in this age. These waves increased in their amplitudes up to 10–12 weeks of age and then gradually decreased in them. It was also demonstrated that the maturation of the EEG in the dog may occur in 20–30 weeks of age, when it is evaluated from the changes of the EEG due to the state of consciousness.—**KEY WORDS:** beagle dog, developmental EEG, NREM sleep.

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The electroencephalogram (EEG) is a record of electrical activity of the brain which provides much information on functional activity of the brain, and one of useful methods to evaluate neurological diseases. The EEG has been used to diagnose brain diseases such as brain tumor, encephalitis and hydrocephalus in small animals [1, 3–7, 16, 18–21]. However, it is well known that the EEG is influenced not only by pathological factors but also by physiological variables, especially the age and the state of consciousness [19]. Therefore it is very important to make a map on the normal EEG in relation to these two physiological variables, in order to evaluate pathological EEG patterns.

Several researchers have reported on the development of the EEG in the dog [2, 9–12, 17]. However, there is no coincidence on the

mature period of the developmental EEG. There is also no report which systematically investigated the relation between the increase of age and the state of consciousness, especially the levels of sleep.

The purpose of the experiment is to analyze visually how the normal EEG, especially that of NREM sleep, of the dog is influenced by two physiological variables, the age and the state of consciousness, in order to establish the criterion of evaluation on the abnormal EEG.

MATERIALS AND METHODS

The 64 beagle dogs which did not show any neurological abnormalities and ranged in age from one day to 8 years of age were used for EEG tracings. They were used several times to record the EEG, and the EEG of two litters was recorded from a postnatal day to the 5th month. Table 1 shows the total number of beagle dogs investigated at each age.

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Table 1. The total number of beagle dogs investigated in each age

Age	Number	Age	Number
1 Day	11	12 Weeks	11
4 Days	11	13	8
7	14	14	7
10	11	15	14
2 Weeks	13	16	7
25	9	17	7
3	11	18	7
4	13	20	14
5	14	23	7
6	13	25	7
7	11	30	11
8	11	35	3
9	16	40	6
10	12	50	8
11	8	50<	<5
Total			300

The electrodes were put under the scalp by means of 27 gauge hypodermic needles. They were enamel-covered copper wires 120 μm in diameter and insulating enamel portions 1 cm in length at their tip were bared by concentrated sulphuric acid and bent back sharply against the needle shafts 0.5 cm long. The electrode placement on the scalp presented by Redding [20] was adopted except for a reference electrode: the left and right fronto-parietal area (LF, RF), and the left and right occipital area (LO, RO). A reference electrode was put on the rhinal bone (R), because the nasal position had less muscular, respiratory and ballistocardiographic artifacts [15]. Montages used are for rhinal reference recordings (monopolar ones) (LF-R, RF-R, LO-R, RO-R) and four bipolar ones (LF-RF, LO-RO, LF-LO, RF-RO), but intrahemispheric bipolar leads (LF-LO, RF-RO) were sometimes omitted to record the electromyogram of a neck muscle and the electrocardiogram, or the electrooculogram. A ground electrode was put under the skin over external occipital protuberance. Eight EEG tracings were recorded simultaneously by an eight-channel polygraph with a rectilinear pen recorder (San-ei Sokki model 142-8 type). The

time constant was 0.3 sec. The standardization signal was 25 $\mu\text{V}/5\text{ mm}$ from birth to the 3rd week of age and 50 $\mu\text{V}/5\text{ mm}$ after the 4th week of age. The recording paper was run at 2.5 cm/sec or 5 cm/sec.

The EEG tracing, as a rule, was obtained without the physical or chemical restraint, but mechanical restraint such as binding the extremities with tapes and covering the eyes was sometimes adopted to eliminate the movement and the muscle artifact. The experimental room which was shielded against alternating current was not sound-proof, so most of EEG tracings were performed at midnight to avoid environmental noises. The EEG recording began when artifacts by dog's movement or muscle activity became rare, and was continued as a rule until the stage of deep sleep was recognized by EEG interpretation. The recording, however, was suspended in three hours, so the EEG of some states of consciousness such as middle or deep sleep could not be recorded in the 10% of total EEG tracings.

RESULTS

Great effort was put on the classification of the developmental EEG in NREM sleep. The following results are mainly EEG classification in NREM sleep from birth to adult.

EEG from birth through 2nd week: The EEG of the 1st postnatal day was characterized by equipotentiality except for occasional appearances of paroxysmal rhythmic waves with a duration of about one second (Fig. 1). The rhythmic waves increased occurrence with days of age and appeared constantly in the first postnatal week. The wave of 7 Hz was also seen at the 4th postnatal day. The EEG of two weeks of age showed two kinds of waves, that is, 7–15 Hz and 5–10 Hz activities (Fig. 2). Behavioral observation revealed that the former waves were seen during wakefulness and the latter during sleep.

EEG from 3rd through 5th week: AT the

Fig. 1. The EEG of the 1st postnatal day and the 7th postnatal day in the beagle dog. The record of the intrahemispheric bipolar leads is omitted. This is also did in the EEG of Fig. 2 to Fig. 8.

Fig. 2. The EEG of wakefulness and sleep recorded on 2 weeks of age in the beagle dog.

Fig. 3. The EEG of wakefulness and sleep recorded on 3 weeks of age in the beagle dog.

Fig. 4. The EEG in wakefulness and at 3 stages of sleep on 5 weeks of age in the beagle dog.

Fig. 5. The EEG in wakefulness and at 3 stages of sleep on 10 weeks of age in the beagle dog.

3rd week of age, the EEG tracings which already showed no equipotentiality occurred in rhythmic waves of 8–13 Hz in the stage of wakefulness, and the two kinds of slow waves were distinguishable during the stage of sleep. The slower ones which appeared after preceding slow waves decreased the rate of occurrence showed frequencies of 3 Hz and amplitudes of 100 μ V, or 1.5 Hz and 200 μ V in some dogs (Fig. 3). The EEG on the 4th week occurred in the waves of 5–7 Hz and 50 μ V in addition to low amplitude fast activity during wakefulness, and much slower waves with amplitudes up to 200 μ V which sometimes contained humps appeared in sleep.

At the 5th week (Fig. 4), the EEG patterns during wakefulness in the dog with opening eyes showed sometimes low amplitude fast waves with 15–20 Hz and 5–15 μ V, the slow waves of 5–7 Hz, or the rhythmic waves of 8–13 Hz. Several minutes after closing eyes, the EEG changed. This stage was classified

as that of light sleep. When the level of consciousness transferred from wakefulness to sleep, the slow waves of 5–7 Hz decreased in their frequencies to 4–6 Hz especially in the occipital area, and the rhythmic waves of 8–13 Hz increased in their amplitudes in the fronto-parietal area. These two patterns, with the evaluation of temporal process of the EEG and behavioral observation, were determined as the first and second phases of light sleep respectively. After light sleep, intermingled with slow waves of 3–5 Hz and 50–100 μ V, humps and rhythmic waves of 5–8 Hz with a duration of one second which became spindles in later period occurred in EEG recordings. This stage, referring to temporal process of the EEG and behavioral observation, was decided as the stage of middle sleep. After passing the stage of middle sleep, large slow waves with frequencies of 2–3 Hz and amplitudes of 100–300 μ V occurred in all over the brain. This stage was categorized as the stage of deep

Fig. 6. The EEG in wakefulness and at 3 stages of sleep on 25 weeks of age in the beagle dog.

sleep. The three stages of sleep, for the first time, were classified in the EEG on the 5th week which occurred in all wave patterns or wave forms such as desynchronizations, rhythmic waves of 8–13 Hz, humps, primitive spindles and large slow waves.

EEG from 6th through 10th week: Desynchronizations with frequencies of 10–30 Hz and voltages of less than 10 μ V became clear in wakefulness on the EEG of 7 weeks of age, which was similar to those seen in the EEG during wakefulness in an adult dog. Except for low amplitude fast waves, rhythmic waves of 8–10 Hz and 30 μ V and slow waves of 6 Hz and 40 μ V were observed during wakefulness. Slow waves of 4–6 Hz observed in the first phase of light sleep during 5 weeks of age developed to rhythmic waves of 4–6 Hz and 30–80 μ V in the 7th week, and increased in the rate of their occurrence in the 10th week (Fig. 5). Irregular high amplitude waves were also seen in the second phase of light sleep. Paroxysmal slow waves, hy-

persynchrony of the EEG [10], characteristic to young animals occurred with stimulation such as sound or light. High amplitude rhythmic waves of 8–13 Hz also occurred at the fronto-parietal area and developed to all areas of the brain, although about a half of the dogs did not show these waves. In middle sleep, spindles and humps became to show their typical wave forms. The former increased the amplitude and the rate of occurrence to maximum, and in some puppies developed the amplitude up to 200 μ V with durations rarely exceeding 1 sec. Humps also increased in amplitudes up to 150–200 μ V. Slow waves observed in deep sleep also increased in voltages up to 400 μ V. The characteristic of the EEG on the 10th week was the maximal development of the rate of occurrence and the amplitudes of waves such as rhythmic waves of 4–7 Hz, spindles, humps and slow waves of 0.5–3 Hz (Fig. 5).

EEG from 11th through 15th week: Maximal amplitudes of each wave seen in the 10th

Fig. 7. The EEG in wakefulness and at 3 stages of sleep in the adult beagle dog.

Fig. 8. The EEG in REM sleep on 4, 5, 20 and 30 weeks of age in the beagle dog.

Fig. 9. Schematic figure of the characteristic wave forms seen in the developmental EEG of the beagle dog. The ordinate is classified by the state of consciousness. The abscissa shows the weeks of age. Solid lines mean that the wave forms occurred in over 50% of EEG tracings, and broken lines do that the wave forms appeared in less than 50% of EEG tracings.

week continued up to 12 weeks of age and then gradually diminished. In the EEG of wakefulness, rhythmic waves of 8–13 Hz and desynchronizations similar to those seen in adult dogs were distinguishable. Slow waves intermingled in the EEG of wakefulness did not diminish by 15 weeks of age. Rhythmic waves of 4–7 Hz in light sleep became sinusoidal rhythmic waves of 6–7 Hz and 50 μ V. Slow waves of 0.5–3 Hz diminished their amplitudes to less than 250 μ V in the 15th week. These changes in EEG tracings suggested that the EEG during this period was going to transfer to that in adulthood.

EEG from 16th through 30th week: Rhythmic waves of 8–13 Hz in wakefulness decreased in rhythmicity, and slow waves observed occasionally in this stage disappeared in the 20th week. After the 20th week no further systematic changes occurred in the EEG in wakefulness (Fig. 6). High amplitude rhythmic waves of 8–13 Hz seen in light

sleep also disappeared after the 20th week. On the other hand, low amplitude waves of 5–10 Hz appeared in light sleep of some dogs of 22 weeks of age, and in that of most dogs over 30 weeks of age. Rhythmic waves of 4–7 Hz seen during light sleep increased in their frequencies and became to contain rhythmic waves of 6–10 Hz and 50 μ V in the 25th week (Fig. 6). The EEG in middle sleep diminished the amplitude: the voltages of spindles became lower than 70 μ V with a duration of less than one sec and humps showed frequencies of less than 3–5 Hz and voltages of less than 150 μ V. The EEG in middle sleep showed little change after the 25th week, but individual differences were seen: in some dogs slow waves occurred in fronto-parietal and occipital areas and in others slow waves were dominant in occipital area. In deep sleep, EEG patterns decreased in amplitudes: 2–3 Hz and 200 μ V in the 25th week (Fig. 6), and 1.5–3 Hz and 150 μ V in

30 weeks of age.

EEG over 31st week: Irregular waves of less than 5–10 Hz and 20 μ V occurred almost continuously, accompanied by the short-lasting waves of low amplitude of 5–10 Hz in light sleep. Rhythmic waves of 4–7 Hz seen in the 25th week were not often recorded after the 30th week. It was also almost impossible from visual interpretation to distinguish the stage of wakefulness from that of light sleep after the 30th week (Fig. 7). Spindles of 14–15 Hz and 30 μ V with a duration of 0.5 sec were difficult to separate from the background EEG, and did not occur in some dogs. The EEG in deep sleep continued to diminish amplitudes, and occurred in slow waves of 1.5 Hz and 100 μ V sometimes without superimposed waves (Fig. 7). After the 51th week, all wave forms became constant.

Development of REM sleep: The separation between REM sleep and NREM sleep became possible after the 2nd week when EEG patterns in wakefulness became different from those in sleep. The EEG in REM sleep in each week of age was similar to that in wakefulness or light sleep on the same week of age (Fig. 8). The distinction between the two kinds of sleep was decided by behavioral changes such as whining or myoclonus-like contractions which occurred frequently in the head or the extremities during REM sleep, and sometimes by the recording of the neck muscle activity and electrooculogram. Slow waves which were seen at the stage of wakefulness or light sleep in early weeks of age were also observed in REM sleep. Changes in the developmental EEG mentioned above are summarized in Fig. 9.

DISCUSSION

It may not be reasonable to classify the EEG showing continuous changes into several stages, but visual interpretation on the EEG provides a fairly accurate estimate of the classification [14]. There has been no re-

searchers who classified the level of sleep into several stages in the developmental EEG of the dog, although that of human beings has been classified. We could, however, distinguish the stage of sleep by the evaluation of the EEG. The stage of middle sleep was easily decided, because humps and spindles were the characteristic waves easily distinguishable from other EEG patterns. Light sleep and deep one were distinguished on the basis of amplitudes and frequencies of waves with a time course of EEG changes. Distinction between wakefulness and light sleep was based on the eyes closing and the change of EEG. When the EEG seen in wakefulness changed after closing eyes, the stage was classified as light sleep.

Slow waves associated with NREM sleep appeared after 2 weeks of age. The onset of this development is coincident with the studies by Fox [10] or Charles and Fuller [2]. It was in the 5th week that the prototypes of all wave forms seen in the adult dog appeared and the level of consciousness could be classified into wakefulness, light sleep, middle sleep and deep sleep. Fox [10] suggested that there are "levels" or varying depths of NREM sleep in 5 weeks of age, although he does not classify "levels". The period from 4 to 5 weeks of age in the dog is marked by relative maturity of the dendritic arborizations [8] and an increase in metabolic rate of the cortex [13].

Charles and Fuller [2] reported that the EEG of the puppy at 8 weeks of age is essentially similar to that of an adult dog. Petersen *et al.* [17] explained that an essentially mature EEG pattern is found at 4 weeks of age and becomes steady during the 7th week. Fox [10] did not indicate the period of EEG maturation, but explained that between 12 and 16 weeks, there is a decrease in amplitude of the EEG but frequency continues to increase into adulthood. Redding [20] insisted that the developmental EEG matures by about 22 to 30 weeks of age, depending on

sex and breed. These discrepancies seem to come from the difference of the criteria for EEG changes in young puppies to an adult pattern. If the immature period of the EEG is defined as the period during which new wave forms occur, the maturation of the EEG in the dog may be 5–6 weeks of age. However, our findings reveal that several wave forms such as the slow wave in wakefulness, the rhythmic waves of 4–6 Hz, the high amplitude rhythmic waves of 8–13 Hz and the slow wave burst in light sleep disappear or diminish in 20 to 30 weeks of age with the reduced frequency of occurrence of the spindle in middle sleep, whereas the low amplitude slow wave in light sleep occurs in 20–30 weeks of age (Fig. 9). Another finding in developmental EEG is that most of wave forms developed their amplitudes and increased their frequencies to the 10th–12th week, and then the amplitudes and frequencies gradually diminished to the 20th–22nd week. These phenomena suggest that the maturation of the EEG in the dog may occur in 20–30 weeks of age. Some wave forms, especially slow waves of 0.5–3 Hz, continue to decrease gradually their amplitudes from 13 weeks to 50 weeks. The increased thickness of bones of the skull and temporal muscles may diminish the amplitudes of EEG recordings.

In REM sleep, Fox [10] has reported that most of sleep in the neonate is REM sleep and NREM sleep is of extremely short duration and is not clearly recognizable until 7–14 days when slow activity increases in amplitude. This is coincident with data of this experiment. It was, however, demonstrated that the EEG in REM sleep were coincident with those in wakefulness or light sleep and the slow waves seen in wakefulness characteristic to young puppies were also observed in REM sleep (Fig. 9).

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要 約

成長にともなうビーグル犬の脳波の変化: 仙波裕之・徳力幹彦¹⁾・佐々木伸雄・竹内 啓・臼井和哉(東京大学農学部家畜外科学教室,¹⁾家畜環境生理学教室)——異常脳波の判定基準を作るために, 64頭のビーグル犬について, 年齢および意識水準の変化に対応する正常脳波の変化を調べた。鼻部に基準電極をおいた単極誘導法(左前頭部-鼻部, 右前頭部-鼻部, 左後頭部-鼻部, 右後頭部-鼻部)と双極誘導法(左前頭部-右前頭部, 左後頭部-右後頭部, 左前頭部-左後頭部, 右前頭部-右後頭部)の8誘導を同時記録した。生後1日にときおり出現した律動波はその後頻度を増し, 1週齢には常にみられた。2週齢では, 覚醒期と睡眠期との判別が脳波上で可能となった。5週齢では, 覚醒期, 軽睡眠期, 中等度睡眠期, および深睡眠期の区別が可能となった。これは, 脱同期, 8-13 Hz の律動波, 瘤波, 初期紡錘波, および 3 Hz 以下の徐波などが5週齢から出現したためであった。これらの波の振幅は次第に増し, 10-12週齢で最大となり, その後は次第に減少した。覚醒期~深睡眠期の脳波の週齢変化から, 脳波が成犬型になる時期は, 20-30週齢であることが明らかとなった。