“COUNTING” OF CLICKS, AS REFLECTED IN AMPLITUDE OF POTENTIALS EVOKED IN AUDITORY CORTEX OF THE DOG

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Abstract. In eight dogs with chronically implanted electrodes click-evoked potentials were recorded in the ectosylvian and suprasylvian gyri. During daily sessions clicks were presented in several short trains with a steady interclick interval of 1 sec and not followed by any unconditional stimulus. The largest amplitudes resulted from the first and last clicks in the series so that curves plotted for each series assumed a U-shape. Changing the intensity or interclick interval disrupted this pattern.

Evoked electrical responses (EPs) of the cerebral cortex have attracted the attention of investigators of higher nervous activity as being relatively standardized phenomena whose changes might reflect the specific processes of cortical activity. The experimental conditions in which these changes are studied may be roughly divided into two groups. The first includes all those tests which deal with changes in EPs during habituation, i.e., during the repetitive presentation of the same stimulus. The other group includes those tests using conditioned reflex procedures, i.e., a stimulus bringing about an EP, combined with presentation of another unconditioned stimulus. In habituation a more or less rapid decrease or weakening of EPs is usually observed (1, 7); whereas the results of experiments with conditioned reflex elaboration are more ambiguous: EPs have been found to increase or decrease but in any case the change in EPs usually increased by the time of reinforcement (2–4, 8). It should be recalled that the difference between these two groups of experiments consists of more than the fact that ha-
Bituation studies employ only one stimulus while conditioned reflex experiments use a combination of stimuli. Another difference is that in the former experiments EP changes are studied during exposure to very long series of identical stimuli (hundreds, thousands or more) while in the latter experiments short trains of an EP-inducing stimulus are usually employed (several to two dozen stimuli per series). There are much less data in the available literature on changes in EPs during systematic exposure of animals to short trains of stimuli without reinforcement. Therefore, in the experiment described, we have studied the changes in EPs in response to short trains of clicks.

Eight dogs with epidurally implanted electrodes were used. EPs were recorded "monopolarly" from the middle ectosylvian gyrus and, in some dogs, also from the anterior part of the suprasylvian gyrus; the indifferent electrode was placed in bone over the frontal sinus. The EEGs were recorded on an Alvar ink recorder and EPs were recorded from the screen of a cathode ray oscilloscope. Concurrently, EPs were recorded on magnetic tape and averaged on a computer. Prior to the experiments, the dogs were habituated to the chamber for 10–15 days, and the experiments started when the dogs stood calmly in the stand.

In the first series of tests, only single clicks of intensity 65 db and 500 ms were presented. The dogs were habituated to the chamber for 10–15 days, and the experiments started when the dogs stood calmly in the stand.

![Graphs showing EEG activity](image_url)

**Fig. 1.** A, EEG of dog 32 at 77 and 79th presentations of a single click, showing the variability of EPs in suprasylvian gyrus (SS) and relative stability in ectosylvian gyrus (ES). B, examples of averaged EPs (15 consecutive responses) in dogs 24 and 32 in which single clicks were presented.
0.16 msec in duration were presented in several sessions, the interval between clicks being varied from 30 sec to 6 min. The amplitude characteristics of the EPs, averaged by computer in sets of 15 sequential stimuli, remained essentially the same from one session to another and subsequently provided a baseline for comparing them with the amplitude of averaged responses to individual clicks in systematically presented trains. Figure 1 shows examples of EPs observed in these tests.

In the second set of tests each dog was presented with a standard train of stimuli (15–20 times in a daily session), consisting of a certain number of (usually 3 or 5) clicks analogous to those used in the first series, each presented at 1 sec intervals. The trains of clicks were presented at irregular intervals varying from 30 sec to 6 min, there being usually no more than 20 trains in a daily session.

The first applications of the trains revealed a considerable diversity of EPs within a train. With further presentations of the standard trains, sometimes by the first session (after 4–6 presentations) but more frequently in the second–fourth sessions (after 30–70 presentations), the amplitudes of the EPs began to acquire a more regular pattern so that the amplitude to the first and last click within the series became higher than the middle (Fig. 2A). Such responses predominated but were not observed in all cases. All dogs, however, exhibited a stage when averaged

![Figure 2](image-url)

**Fig. 2.** A, EEG of middle ectosylvian gyrus of dog 24 at 20th presentation of a series of 5 clicks. B, averaged EPs from the same test. I–V, averages for response according to position in series of five.
responses distinctly showed that the amplitude of EPs in the specific auditory cortex in response to middle clicks was smaller than to the largest ones (Fig 2B). Figure 3 shows the graphs of amplitudes of the different components of EPs for sequential responses to clicks within the trains plotted from the results of averaging the EPs to clicks of 15 consecutive series. EP amplitudes in a train at first decreased and then again increased, resulting in a U-shaped graph. In a series of five clicks, the lowest amplitude was observed in some dogs in the 3rd response, and in others in the 2nd or 4th response. The difference in amplitudes of the extreme and middle responses, i.e., the “depth” of the U-shape pattern, decreased somewhat as tests were repeated. In some dogs, however, such a flattening did not occur even after 10–15 sessions (200–250 presentations of the trains). A long interval between experimental sessions usually strongly flattened the U-shape pattern and several sessions were required to restore its original shape. However, the U-shape pattern was sometimes more marked in a series following a prolonged interval between sessions. In most cases peak amplitudes of the initial and late EP components behaved much the same. An orderly arrangement of the amplitudes was also observed in EPs of the
associative cortical area (see Fig 3). These results suggest that as the standard trains of clicks were repeated a generalized appraisal of the trains was elaborated and the character of EPs to an individual click depended on its position within the train.

To check the validity of this suggestion, the number of clicks presented within a train was changed for several dogs. This altered the U-shape pattern of amplitude changes in the trains. Figure 5 shows graphs describing relations among the EP amplitudes depending on a change in the number of clicks within a train. Thus, in dog 24 presented with a train of 5 clicks, the lowest EP amplitude was observed in response to the 3rd click (Fig. 5A); however, when a train of 3 clicks was systematically presented instead, the amplitude of the 2nd response decreased and that of the 3rd increased (Fig. 5B). In dog 31, substitution of a systematic train of 5 clicks by another consisting of 10 clicks, altered EP relations in the train, as can be easily seen in Fig. 4. Since

![Graphs of averaged (by sets of 60) summated peak amplitudes of EPs in dog 31 (see text for details). A, filled circles, systematic presentations of a 5-click series; open circles, systematic presentations of a 10-click series. B, filled circles, presentation of a 5-click series; open circles, the first 15 presentations of a 10-click series. Ordinate, amplitude in relative units; abscissa, consecutive EPs of the series.](image)

the amplitudes of early and late EP components in the series showed similar changes (see Fig. 3 and 5), the graphs of Fig. 4 are plotted from the sum of averaged peak amplitudes of early and late EP components. When a series of five clicks was used, the lowest amplitude of the EPs to the fourth click was observed and there was a substantial difference between the 4th and 5th response. Changes in responses to a 10-click train consisted in a strong diminution in amplitude of the 2nd response and in levelling out of responses 3 to 8 which became approximately equal to the amplitude of the 4th, the smallest response. Finally, the 9th response almost equalled in amplitude to the last response in the 5-click
trains. It is of interest that the 10th response, while being greater than the average amplitude for the whole train of clicks was somewhat smaller than the 9th (Fig. 4A). Such relations among responses in these long trains were established not at once, but only after several dozens of presentations. As shown by the averaging of EPs in the first 15 presentations of the 10-click trains (Fig. 4B), responses to the first five click of these long trains differed but slightly from those observed when the short trains were used.

A dependence of EP amplitudes on the position within the train of clicks was also observed in the auditory cortex of cats trained under similar experimental conditions.

The above described dependence of EP amplitudes on the serial number of the click suggests that the amplitudes of EPs are determined by the elaborated integral generalized appraisal of the length of the entire train of clicks. As follows from the graphs of Fig. 5A and 5B,

![Graph of peak amplitudes of averaged EPs in dog 24 for a 5-click series (A). Same graph of a 3-click series (B), Designations as in Fig. 3.](image)

the amplitude of EPs to the 3rd click of the series in dog 24 depended not only on the 3rd position of the click in the train, but also on whether or not the click was to be followed by others. The same was true for the 2nd and 5th responses in dog 31 (Fig. 4A).

The U-shaped pattern of changes in EP amplitude in response to sequential clicks has the following properties; (i) it requires repetitive applications of trains for its formation; (ii) it becomes weaker, and may disappear altogether when there is a prolonged interval between ex-
experimental sessions; (iii) its configuration alters as a result of a change in the series length. These properties unequivocally suggest that this phenomenon has a conditioned reflex nature.

In the experiments described above, an integration of a signal series occurred. However, each individual signal in the series was processed separately in relation to its serial number. Because no other stimulation except clicks was used in the experiments, the elaborated reaction may be considered to be a variant of the local conditioned reflex, which, according to Asratyan (1), is characterized by the fact that it is based on connections between the elements of the system excited by the same stimulus. Whatever the case, we think that the described phenomenon may be regarded as an elementary model of counting.

The morpho-functional structure of this phenomenon remains obscure. It may be expected that both the properties of the stimuli and interstimulus intervals are instrumental in its formation. We have made an attempt to clear up this question, but have succeeded only in part. For this purpose, either the characteristics of the stimuli or interstimulus intervals were changed in several dogs after definite relations among the parameters of sequential EPs had been established by the systematic presentation of a series of clicks.

Some dogs were presented with a series of clicks in which the intensity of the clicks was changed. The initial intensity of 65 db was either increased to 75 db or decreased to about 52 db. All dogs exhibited changes in the integrative curve, i.e., in the relations among averaged EPs to consecutive clicks of the series, when the sound was increased as well as decreased. Figure 6 shows one example of such changes.

Fig. 6. Graphs of averaged (by sets of 15) peak amplitudes in dog 31. A, click 65 db; B, click 52 db; C, return to initial intensity. Open circles, suprasylvian gyrus; filled circles, ectosylvian gyrus.
Before a change in intensity, variations of EP amplitudes in the specific cortical area in response to sequential clicks were described by a U-shaped curve with some rise of amplitude in response to the third click. Similar changes in responses were noted in the associative cortex. When the intensity of the clicks was changed, the pattern of EP amplitudes in the series altered in both areas; however, while in the specific cortex the responses were somewhat more homogeneous the responses in the associative cortex were considerably increased. Although the characteristics of averaged EPs invariably changed with change in intensity, the pattern of changes in the response curve was in many cases different from that shown in Fig. 6. In fact, only two phenomena were consistently observed: a change in the relations of EP amplitudes in the trains of stimuli and a difference in the character of such changes between the specific and associative cortical areas, the amplitudes in the associative cortex being greater in nearly all cases. If clicks of different intensity continued to be systematically applied in subsequent tests, the initial pattern of relations among EP amplitudes was usually more or less restored (Fig 6C), though it was not so distinct as when the initial intensity was used.

Following the establishment of stable relations among EP amplitudes characteristic for each dog in a series with an interstimulus interval of 1 sec, the same series was systematically applied in three dogs with an interstimulus interval of 500 msec. As in the case of a change in click intensity, a change in intersignal interval altered the integral curve in both areas, though to different degrees. In the course of further systematic presentations of series with an interstimulus interval of 500 msec, characteristic relations among amplitudes of averaged responses

![Fig. 7. EEG of dog 29 presented with a train of clicks with different intersignal intervals. A, intersignal interval of 1 sec; B, intersignal interval of 500 msec; C, intersignal interval of 2 sec. 1, suprasylvian gyrus; 2, ectosylvian gyrus; 3, clicks.](image-url)
in the series were established only in one of the three dogs (Fig. 7). In this case the EEG is much more flattened and contains higher frequencies with an interstimulus interval of 500 msec. A sharp desynchronization with decreased amplitudes occurred also in two other dogs throughout the period when the 500-msec interval was used.

With the use of an interstimulus interval of 2 sec, on the contrary, the EEG of all dogs showed lower frequencies and some increase in amplitude (Fig. 7C). With this frequency of clicks in the series, the dogs more readily established the relations between amplitude characteristic for the series with 1-sec intervals. However, with this interval too, these relations were at times disrupted.

The present experiments warrant the following conclusions:

1. Any change in parameters of the train of stimuli results in a disturbance of the EP relations established for a given series.

2. Further systematic application of an altered series may restore the distribution pattern of EP amplitude in the series.

3. Both the elaboration of a U-shaped pattern of EP amplitude variations in the standard series and the alterations of this pattern within changes in the parameters of the series are observed to different degrees in the specific auditory and the associative cortical areas.

What, then, may be the cause of alterations in EP relations within the series after changing the stimulus parameters? Such alterations, we believe, may either reflect the actual impairment of the evaluation of the series or result from the masking effect of the orienting response evoked by the signal changes. It may be assumed that the process of appraisal of the series occurs as before, i.e., the signals are "counted off", but it is difficult to study this process on the basis of EP parameters because of the disorganizing influence of the orienting response.

More difficult is the interpretation of the evidence concerning the changes arising upon shortening or prolonging the interval between clicks within the series. Indeed, it may be assumed that the integration of a systematically presented series primarily involves the appraisal of its total length, i.e., of the time during which the given series lasts. It cannot be ruled out that this time is broken down into certain periods having different significance, in much the same way as, for example, in the case of active and inhibitory phases of delayed conditioned reflexes (5). The clicks which are presented during different stages or phases of the time period of the whole series enable us only to test the occurrence of these phases from the EP parameters. When the interstimulus interval is changed, clicks occur during other phases formed in the course of repetitive presentations of the previous series, and characteristics of other periods thus appear in EP parameters.

The U-shaped pattern of EP changes may be thus restored only when
the conditioned reflex appraisal of the time of action of the series with a new interstimulus interval is established. On the other hand, abstracting, recognition of the absolute number of stimuli may be thought to take place; and in this case one may expect that the established relations among EPs may be readily restored in the series with different interstimulus intervals because the number of stimuli in the train of clicks did not change (this was observed in one of our dogs). This may suggest that different animals may "utilize" different properties of the presented standard train stimuli for their integration, either primarily the time or the absolute number of stimuli. In an unpublished study of I. N. Tveritskaya, in which dogs had to differentiate a single (non-reinforced) click from a series of two identical clicks (reinforced by electrocutaneous stimulation of the paw), three of six dogs based their responses on the number of stimuli and three others on the onset of the first stimulus. The very possibility of using the number of stimuli as the basis for such afferent synthesis becomes more likely in the light of the data reported by Thompson et al. (6) which indicate that the associative cortex contains cells which respond only to a definite number of stimuli specific for a given cell.

REFERENCES


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