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GROWLING COMPONENT OF VOCALIZATION AS A QUANTITATIVE INDEX OF CARBACHOL-INDUCED EMOTIONAL-DEFENSIVE RESPONSE IN CATS

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Key words: cat, defensive response, hypothalamus, carbachol, eye movements, vocalization, emotional response

Abstract. Vocalization and eye movements during emotional-defensive response evoked by unilateral intrahypothalamic carbachol injections (10 μg) were quantitatively determined. The growling episodes duration paralleled the development and the subsiding of the defensive behavior, while the changes of eye movements indicated rather a general arousal than the course of agonistic attitude. The growling component can be treated as (i) a specific form of vocalization for emotional-defensive response, (ii) quantitative intensity index of the response, and (iii) a value reflecting the dynamics and the time-course of the emotional state, unlike the hissing component which is inappropriate for quantitative determination. The results enable to treat the carbachol-induced response as a model for quantitative investigations on emotional-defensive states in cats. The vocalization changes compared with cardiovascular changes are discussed in terms of their usefulness in measurements of aversive emotional responses.

INTRODUCTION

Intrahypothalamic carbachol (CCh) injections in unprovoked cats elicit a characteristic emotional-defensive response, described earlier (11). The induced defensive state can be easily defined on the basis of gross behavioral changes and a characteristic set of manifestations, however, it is difficult to find a single sign indicating beyond doubt the animal's emotional state. As Brady (8) stated, observations of a single sign are hardly likely to be sufficient for determining the whole behavior. However, attempts may be made to find a measurable feature, with changes parallel changes of the emotional state, which would be correlated with this state.

The investigation of the frequency of appearance of particular response components after intrahypothalamic CCh microinjections in cats revealed that a general arousal and the animal's attention as well as a characteristic vocalization were elicited in all cases (11). Earlier investigations of the CCh-induced response (14, 16, 24, 29) demonstrated that the characteristic vocalization of cats was a useful correlate for quantitative determination. The magnitude of the vocalization expressed by its duration can reflect both the rate of response increase and the dose-response relation (16, 20, 29). Further investigation provided some evidence that CCh-induced response had a complex course (20). Vocalization appeared to be the fastest changing sign following the injection, while general arousal underwent slow changes. It seemed to be purposeful to undertake a quantitative estimation of the CCh-induced response on the basis of measurements of both slowly and fast changing manifestations. The vocalization, mainly growling, is an easily measurable manifestation, while general activation presents some difficulties as far as quantitative determination is concerned, so it was decided to monitor it by the recordings of eye movements.

Thus the aim of the present paper consists in: (i) measurements of vocalization and eye movements as behavioral patterns appearing with the greatest probability in emotional-defensive response induced by intrahypothalamic CCh injection; (ii) investigation of the dynamics and time course of the measured values.

MATERIAL AND METHODS

The experiment was performed on 22 adult cats of both sexes (16 females, 6 males), with 1.8–3.2 kg body weight. Stainless-steel cannulas, 1 mm in diameter, were stereotaxically implanted into the antero-medial hypothalamus and preoptic area ($F = 13.5$, $L = 1.5$; 2.0; and $H = -3.0$ according to Jasper and Ajmone-Marsan's (19) atlas) in all cats. Each animal possessed two bilateral outer cannulas. An injection cannula connected with a microinjector syringe (E. Zimmermann, Leipzig) was intracerebrally introduced through a guide cannula. Carbachol (carbamylcholine chloride, Fluka-Buchs) dissolved in 0.9% NaCl solution was administered in 5.0–10.0 μg doses and 2.0 μl of volume. Each cat was injected not more than once a week. Other details concerning experimental subjects, stereotaxic operations and microinjection technique were described earlier (11).

Eye movement recordings were carried out by means of 0.2 mm diameter stainless steel electrodes with 2 mm uninsulated circle-shaped ends. They were placed bilaterally in medial position above the eyes, under the upper wall of the orbites. The electrodes were introduced through the frontal sinuses which were subsequently filled with methacrylate resin (Duracryl Special, Spofa, Prague). The placement of electrodes enabled us to record mainly horizontal eye movements which, as indicated by a preliminary observation, were predominant in the evoked response. Eye movements were recorded on the 8-channel electroencephalograph (EEG 8.111, Messgerätewerk, Zwönitz), and the obtained electrooculograms were used for quantitative analysis (Fig. 1). The measurements consisted in counting up the number of eye movements and the evaluation of the maximal amplitude and the angular velocity of these movements in minute periods of time during 30 min, according to the method described by Latkowski (22). The angular velocity of eye movements was expressed by means of a single eye movement duration.

The characteristic vocalization of cats (growling and hissing) was recorded on a tape recorder and on electroencephalograph with the use of a microphone (working frequency range 70 Hz–15 kHz) hung up under the ceiling of the chamber. In accordance with the method developed earlier (29), the measurements of growling consisted in summing up the number and duration of separate vocalization episodes (growls, Fig. 1) during 30 min of observation. Two coupled electromechanical digital counters were employed for this purpose. The first of the counters, operated manually, summed up (with accuracy to 0.1 s) the duration, while the second summed automatically the number of impulses.

The greater part of the present paper comprises the measurements performed on cats whose behavior, as well as the experimental situation, were described previously (11). During the recording period the experimenter sat all the time 1–1.5 m away from the cat and his activity was merely to operate the recording apparatus. Nobody else approached the chamber during observation, and the animals were not provoked by any means. The remaining methodical details together with the histological verification were given in the previous paper (11). All the microinjection points are schematically drawn up in separate figures. In the statistical evaluation of the results the correlation test and the multifactorial analysis of variance according to Volk (30) were applied.

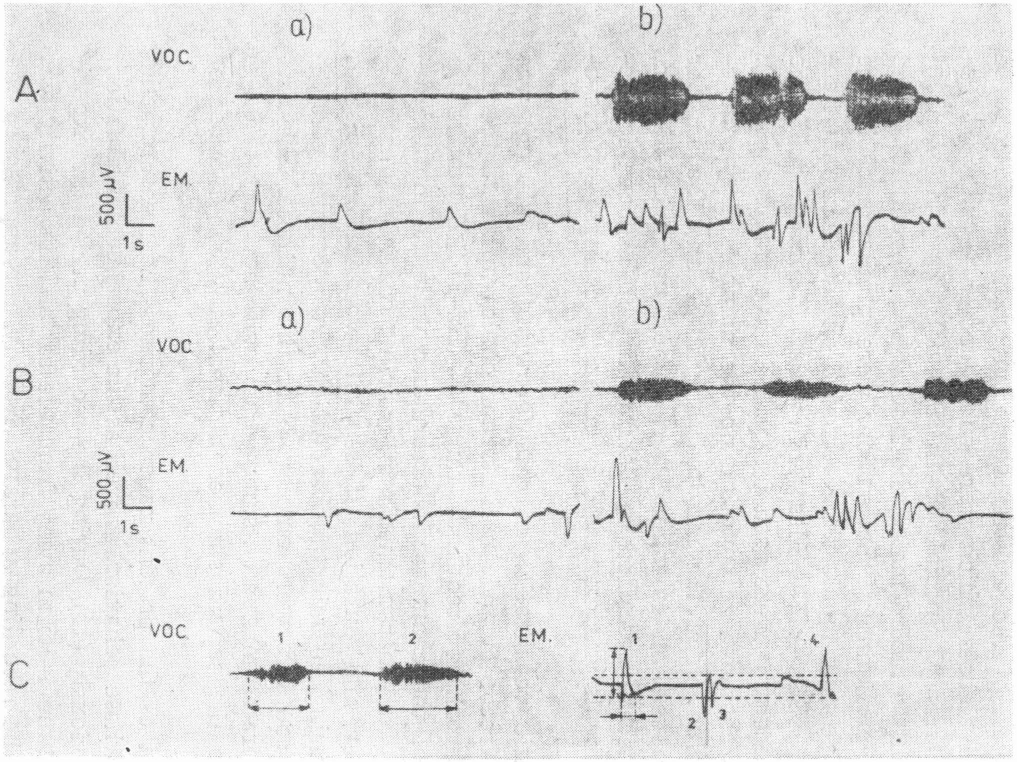


Fig. 1. Polygraphic recordings of vocalization (VOC) and eye movements (EM) before (a) and after (b) unilateral intrahypothalamic injection of CCh (10 µg); *A*, fragment of strongly expressed response 16 min after injection; *B*, weakly expressed response 6 min after injection; C, scheme illustrating quantitative determination of VOC and EM. Duration of separate growls (long horizontal arrows) and number of growls (1–2) were summed up during the 30 min of observation. Quantitative determination of EM consisted in counting up the number of EM (1–4) and evaluating the maximal amplitude (vertical arrow) and single eye movement duration (short horizontal arrows) according to Latkowski's method (22).

RESULTS

Eye movements

The typical emotional-defensive response developed after microinjections of CCh (5.0–10.0 μg) into the anterior hypothalamic and preoptic region. During the first few minutes a strong arousal and attention response appeared in all cases. At first the cats began to stare quietly at different objects and examined them attentively; however, their eyes moved more frequently than in the control period. Some minutes later the arousal increased, which was reflected in all measured parameters (Fig. 2). The electrooculogram indicated an alertness pattern, initially in repeated episodes and later in a continuous form. Some responses were marked by a moderately regular record, on which an alternately changing eye movement direction, appearing in short series, could be seen. A considerable portion of records contained less regular changes of a type approximating nystagmoidal character with occasional eyeball floating. Short episodes of nystagmus occured rarely, but persisting clear-cut nystagmus was observed only in one case.

The number of eye movements per time unit slowly increased. This increase was accompanied by intensifying horizontal head movements (looking round), sometimes alternately to the left and right. The measurements of maximal amplitude and mean duration of single eye movements (Fig. 2) in successive one-minute periods showed that the angular deflexion of the eyeballs had a tendency to increase, and the duration of single movements tended to decrease. Thus the angular velocity of eye movements gradually increased. The changes of eye movement number were the most pronounced and characterized by the greatest stability and for this reason they were regarded as the most representative for the measuring of eye movements. It is worth mentioning that the quantity, the amplitude, as well as the velocity of eye movements had a tendency to increase during the whole 30-minute period of observation. The emotional-defensive response was gradually diminishing until it discontinued completely in the last minutes of the recording period, while all the measured eyeball movement parameters still had an increasing tendency.

Growling

Vocalization was found to be one of the constant and characteristic response components induced by CCh injections. It consisted of growling and hissing. Repetitive and regular growling was an inseparable, integral element of the emotional-defensive response. Figure 3 illustrates the number of growls, the total time of growling, the duration of single

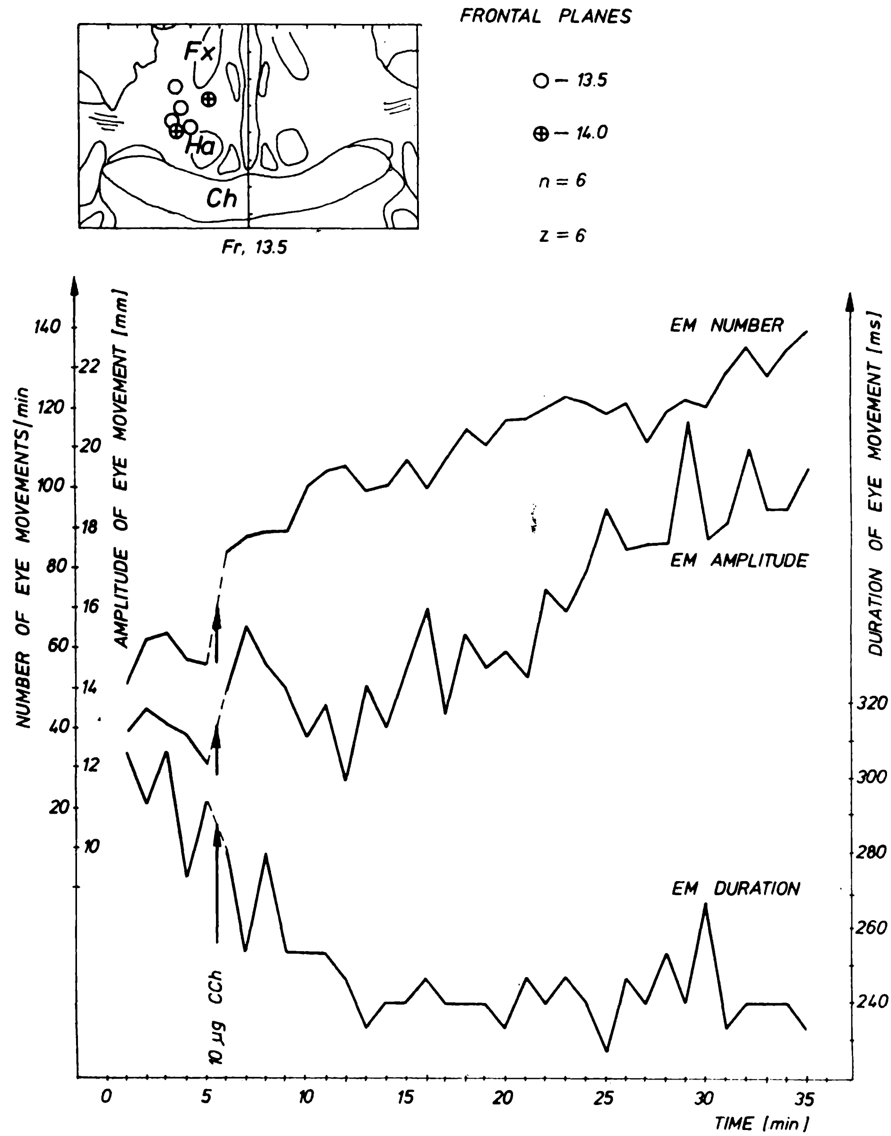


Fig. 2. Time-courses of the eye movement (EM) parameters (EM number, EM amplitude and EM duration) from the same experimental sessions before and after unilateral intrahypothalamic injection of CCh (10 µg). Initial section of each plot reflects 5 min control period preceeding injection (arrow). Localization of all involved injection points is indicated at the top of the Figure in the frontal plane 13.5 according to Jasper and Ajmone-Marsan's stereotaxic atlas (19). Points located rostrally or caudally to this plane are marked with different signs. Abbreviations: *n*, number of experimental sessions; z, number of animals; Ch, optic chiasm; Fx, fornix; Ha, anterior hypothalamus.

growls and the amplitude of growls, in their time-course in respective one minute periods of the response. Only the experimental sessions during which the cats did not manifest locomotion and did not modify their positions in relation to the microphone during the whole time of the recording were chosen for growling evaluation.

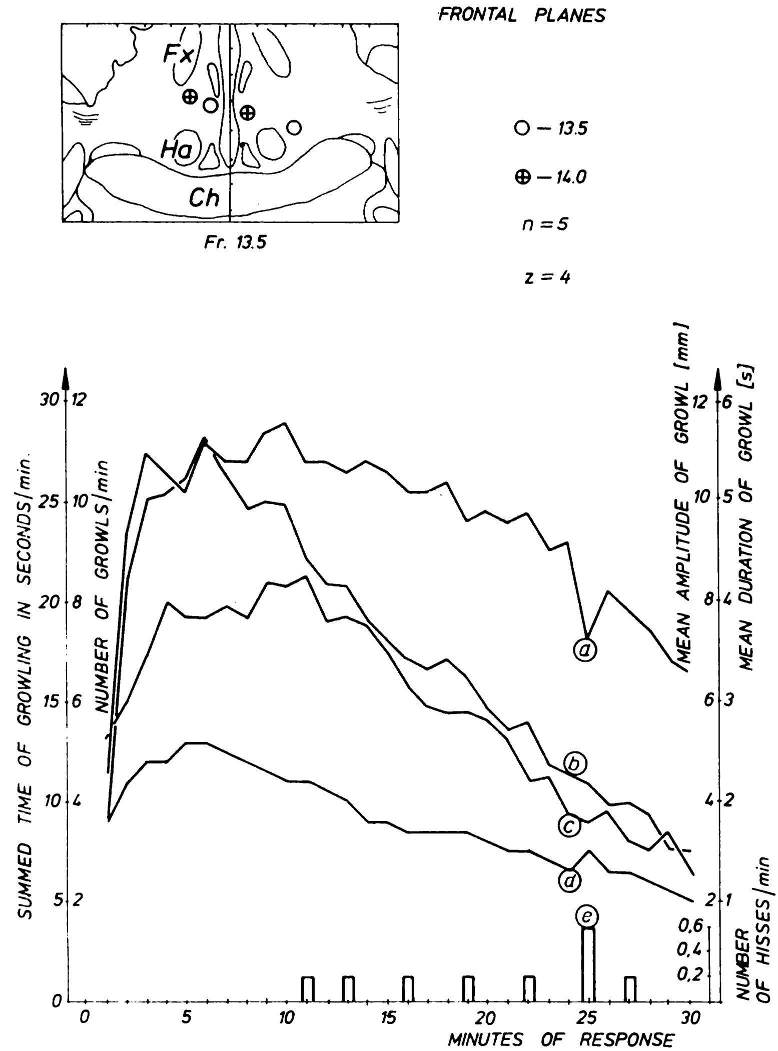


Fig. 3. Time-courses of vocalization parameters (*a–d*, growling and *e*, hissing) after unilateral intrahypothalamic injection of CCh (10 μg). All parameters were measured in 1 min intervals. The first minute on the time scale is the first minute of the response regardless of latency period; *a*, number of growls; *b*, time of growling; *c*, amplitude of growl; *d*, duration of growl; *e*, number of hisses. Other denotations as in Fig. 2. See text for statistical evaluation.

The first four minutes of the response were distinguished by a rapid increase in growling as indicated by all the recorded parameters. During the next four minutes (5–8th min) the values of the parameters remained at peak level for some time and then gradually decreased.

It has to be pointed out that the time-course of growling reflected well the changes in the emotional-defensive behavior of the cat during 30 min of observation. Especially curves showing single growls duration and amplitude changes as well as summed-up growling time changes clearly illustrated the initial explosion of the response and its slow gradual decline.

A correlation study of mean values of each parameter paired with each of the others ($n = 30$) demonstrated in all cases a highly significant positive correlation ($r = 0.68$ to 0.92; $P < 0.001$). However, the correlation study of individual values of each parameter paired with each of the others ($n = 150$) proved that the number of growls and the mean duration of single growls did not show a significant correlation ($r = 0.01$; $P > 0.05$), and the number of growls and the mean amplitude of single growls showed the correlation at the level $P < 0.02$ ($r = 0.20$). All other parameter combinations demonstrated a highly significant correlation at the level $P < 0.001$ ($r = 0.59$ to 0.71). All the measured parameters seem to be related and to reflect in a certain way the changes of the emotional state. The lack of statistically significant correlation between the number and the mean time of single growls could have been caused by the fact that increasing respiration rate modified each of the parameters in a different way. The values which reflect best the vocalization changes as well as the time-course of emotional-defensive response seem to be the minute sums of growling time and, to a smaller extent, the minute numbers of growls.

Hissing

Each emotional-defensive response was accompanied by growling, while hissing occurred occasionally. As Fig. 3 illustrates, hissing appeared irregularly and, as a rule, after greater latency than in the case of growling. It was very rare that hissing had its time-course approximated to that of growling, but it happened very often that an animal hissed intensively during one session and did not display this pattern during the next one at the same dose level. Hissing appeared even at a slight unintended provocation, and could be still present for some time after discontinuation of spontaneous growling. Distinct spontaneous hissing (more than 5 hisses per 30 min) appeared in 25% of experimental sessions.

General observations indicated that the spontaneous hissing appeared during the most strongly expressed and intensive emotional-defensive responses. However, the investigation of the relationship between the level of growling (total time of growling per 30 min) and the number of hisses per 30 min indicated no statistically significant correlation between these values ($n = 34$, $r = 0.22$; $P > 0.2$). Hissing did not reflect either the response level or its time-course. Thus, hissing cannot serve the purpose of quantitative determination of the emotional-defensive response induced in described conditions.

Relationship between the magnitude of vocalization and latency or response duration

The relationship between the vocalization magnitude and the duration of the emotional-defensive response is illustrated in Fig. 4. The vocalization was measured by total sums of the number of growls and growling time from 30 min of the session. The response duration was determined on the grounds of spontaneous vocalization decline. Vocalization was regarded as discontinued when it did not appear for a longer period of time than three successive minutes of observation.

The analysis revealed a statistically significant positive correlation between the response duration and sums of both the growling time ($n = 80$, $r = 0.74$; $P < 0.001$) and the growl number ($n = 80$, $r = 0.62$; $P < 0.001$). The obtained data proved that the longer is the duration of the emotional-defensive response, the greater is the vocalization measured in steady fixed periods of time. The vocalization level can illustrate the intensity of the emotional-defensive response and may be, within some limits, an index of its duration.

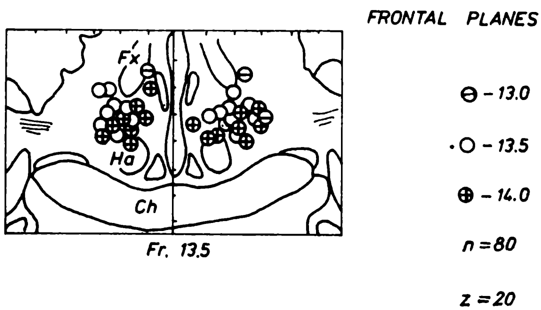
The comparison of the vocalization magnitude with the response latency (Fig. 5) revealed a highly significant negative correlation between these values, concerning both the sums of growling time ($n = 80$, $r = -0{,}57$; $P < 0.001$) and growl numbers ($n = 80$, $r = -0.54$; $P < 0.001$). Thus responses with high vocalization level started as the earliest.

On the basis of obtained results it may be assumed that emotional-defensive responses with intensively expressed set of behavioral components were accompanied by a higher level of vocalization and that they lasted longer than weakly expressed responses.

Time-course of responses at different intensity levels

The presented results point out that intensively expressed emotional-defensive responses were characterized by a short latency, while slightly expressed reactions required a longer period of time to appear.

Therefore all investigated responses were divided according to their latency periods into 5 classes, and vocalization time-courses were investigated in these groups (Fig. 6*A*, *B*, *C*). The latency periods increased exponentially in successive classes. Not more than 10 experimental sessions were chosen at random for every class (in all $n = 45$). The ranges and quantities of particular classes are shown in Fig. 6.



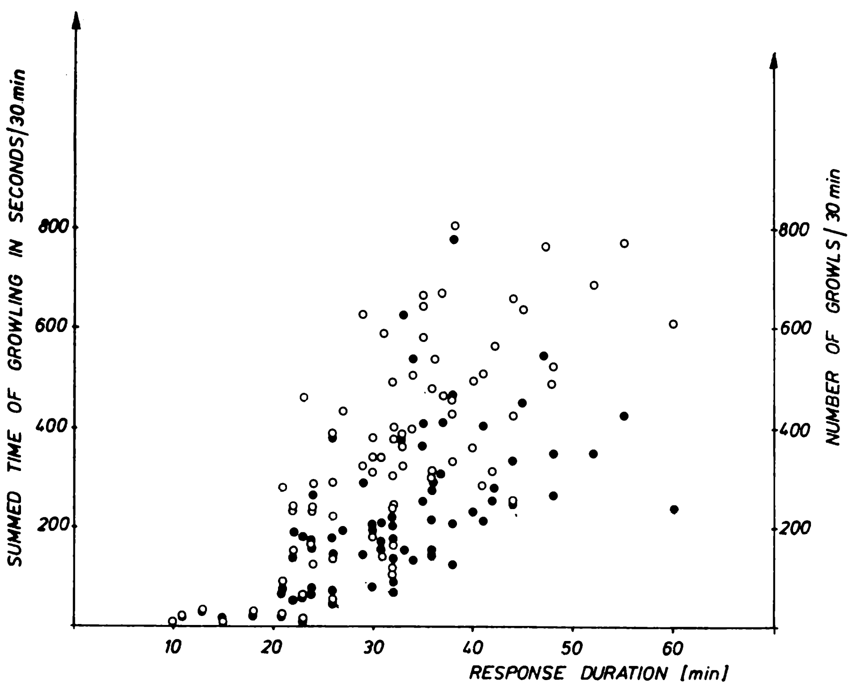
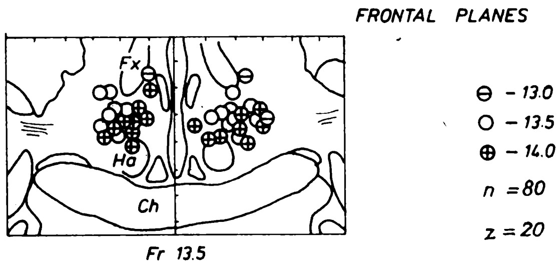


Fig. 4. Relationship between the vocalization magnitude and the duration of the response induced by unilateral intrahypothalamic injection of CCh (10 μg); open circles, time of growling; filled circles, number of growls; Other denotations as in Fig. 2. See text for statistical evaluation.

The vocalization time-courses revealed a clear-cut gradation for different latency classes. Two-dimensional analysis of variance confirmed that the differences of response levels (latency factor) are highly significant, both for growling time ($F = 9.58$, $df = 4/40$; $P < 0.001$, Fig. 6*A*) and for the number of growls ($F = 7.69$, $df = 4/40$; $P < 0.001$, Fig. 6*B*). The study of the effect of time factor on the course of the measured



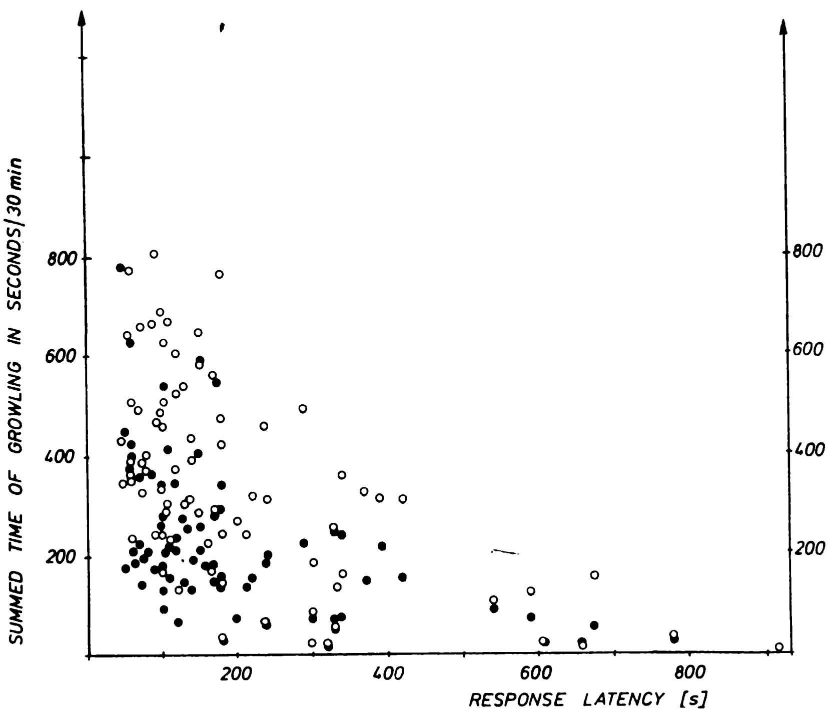


Fig. 5. Relationship between the vocalization magnitude and the latency of response induced by unilateral intrahypothalamic injections of CCh (10 μg); open circles, time of growling; filled circles, number of growls; Denotations as in Fig. 2. See text for statistical evaluation.

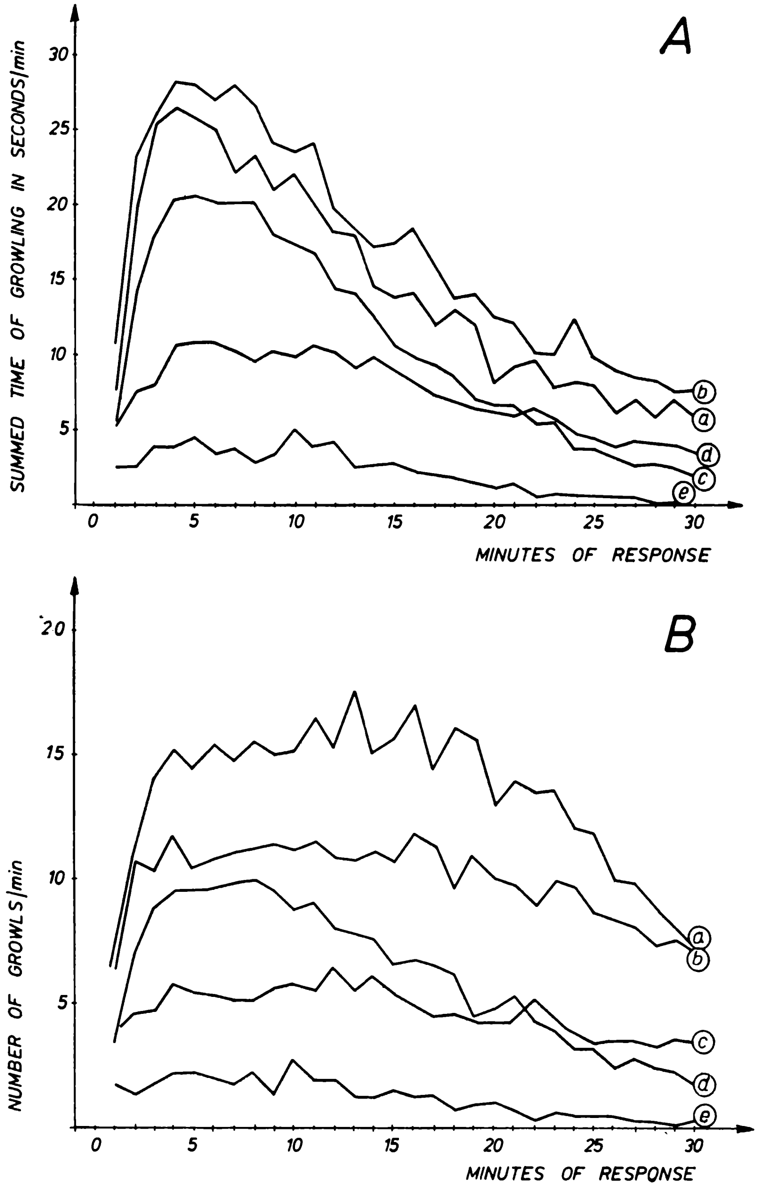
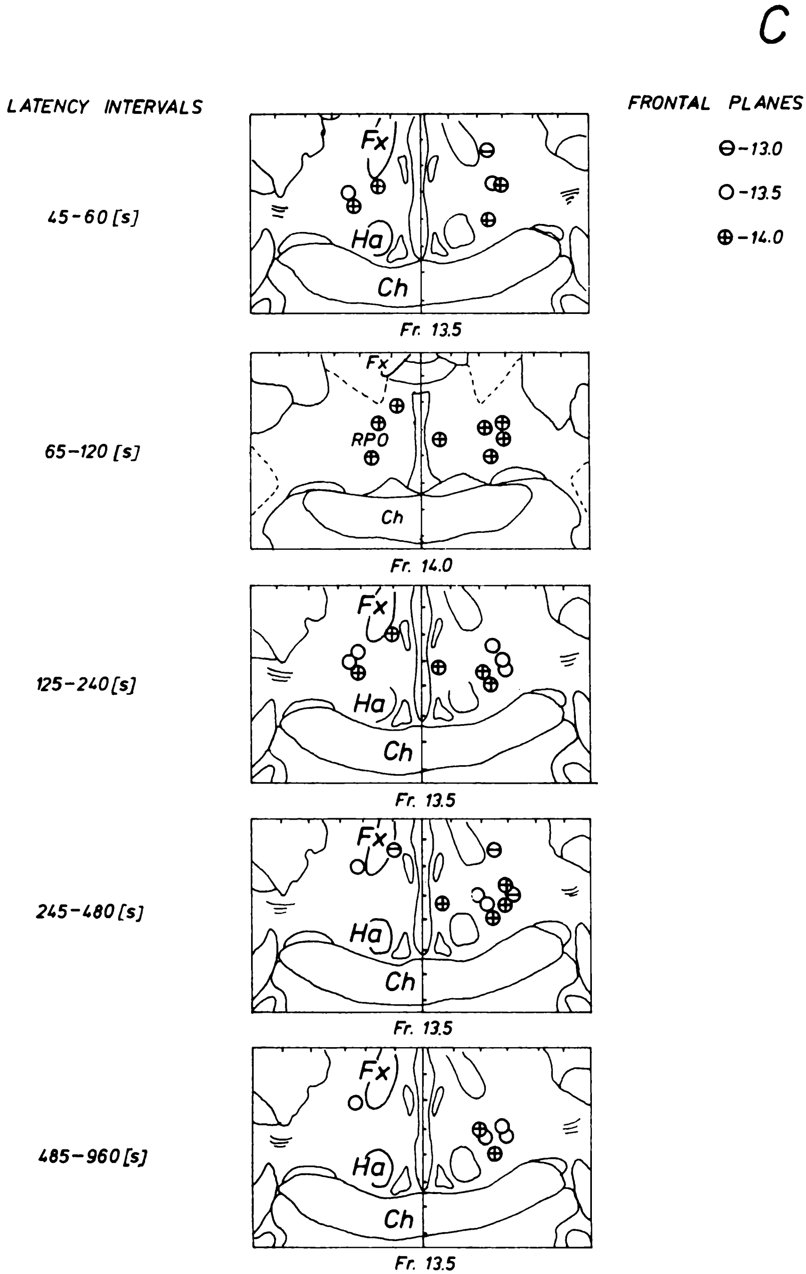


Fig. 6. Time-courses of vocalization in five classes of responses induced by unilateral intrahypothalamic injection of CCh (10 μg). The classes were categorized with respect to response latency. The latency periods are increasing exponentially in particular classes: *a*, 45–60; *b*, 65–120; *c*, 125–240; *d*, 245–480; *e*, 485–960 s; *A*, time-courses of growling time values; *B*, time-courses of growling number values; *C*, localization of all involved injection points in successive latency classes. Other denotations as in Fig. 2. See text for statistical evaluation.


C
LATENCY INTERVALS
FRONTAL PLANES
⊖-13.0
○-13.5
⊕-14.0
45-60 [s]
Fx
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Ch
Fr. 13.5
65-120 [s]
Fx
RPO
Ch
Fr. 14.0
125-240 [s]
Fx
Ha
Ch
Fr. 13.5
245-480 [s]
Fx
Ha
Ch
Fr. 13.5
485-960 [s]
Fx
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values revealed also its highly significant influence in respective 5min block (6 blocks of time), analogically for growling time ($F = 36.93$, $df = 5/200$; $P < 0.001$) and the number of growls ($F = 9.58$, $df = 5/200$; $P < 0.001$). These findings mean that the course of a response in initial periods of time significantly differs from that in further periods of time. Moreover, the character of the course of growling time is different at particular analysed latency levels (significant interaction between latency and time factors, $F = 2.17$, $df = 20/200$; $P < 0.01$). Curves for intensive responses increased violently reaching high values and decreased sharply, while low level responses were distinguished by relatively uniform low value courses, and declined gently (Fig. 6*A*). No such relationship was found for particular levels of growl number (nonsignificant interaction between latencies and blocks of time). In this case the time factor influenced similarly the changes of growl number at different latency classes.

The presented results indicated that growling time summed up in minute intervals reflected not only the response intensity but also the dynamics of the response course.

Comparison of time-courses of eye movements and vocalization values

The number of eye movements and vocalization changes recorded simultaneously during the same experimental sessions in the same cats are presented in Fig. 7. The time-courses of measured values revealed two different processes: the permanent increase of arousal during the observed period of time, reflected by eye movement number and, after a sudden rise, the permanent decrease of the vocalization time together with aversive emotional-defensive excitement. This excitement was expressed by a change in agonistic and aversive attitude towards environmental cues and subsided paralelly to vocalization. The comparison of these two processes enable us to split the elicited response into two consecutive phases: (i) the first, lasting 8–12 min, characterized by violent development and persistence of the response and by an increase of all the parameters measured; (ii) the second, distinguished by the decline of both aversive arousal and vocalization, with a simultaneous maintenance or even increase of general arousal, expressed by a greater number of eye movements and, in some cases, by locomotion.

The investigation of a correlation between the eye movement number and growling time data for all the obtained values (Fig. 7) revealed the lack of significant correlation ($n = 660$, $r = -0.07$; $P > 0.05$). The comparison of changes of the eye movement number with changes of the growl number showed a significant positive correlation ($n = 660$, $r = 0.19$; $P < 0.001$) in spite of the fact that the time course changes of eye movements did not reflect the dynamics of the emotional-defensive response. The changes of the growl number seem to exhibit common features both with changes of growling time (see Fig. 3) and with eye movement number (Fig. 7).

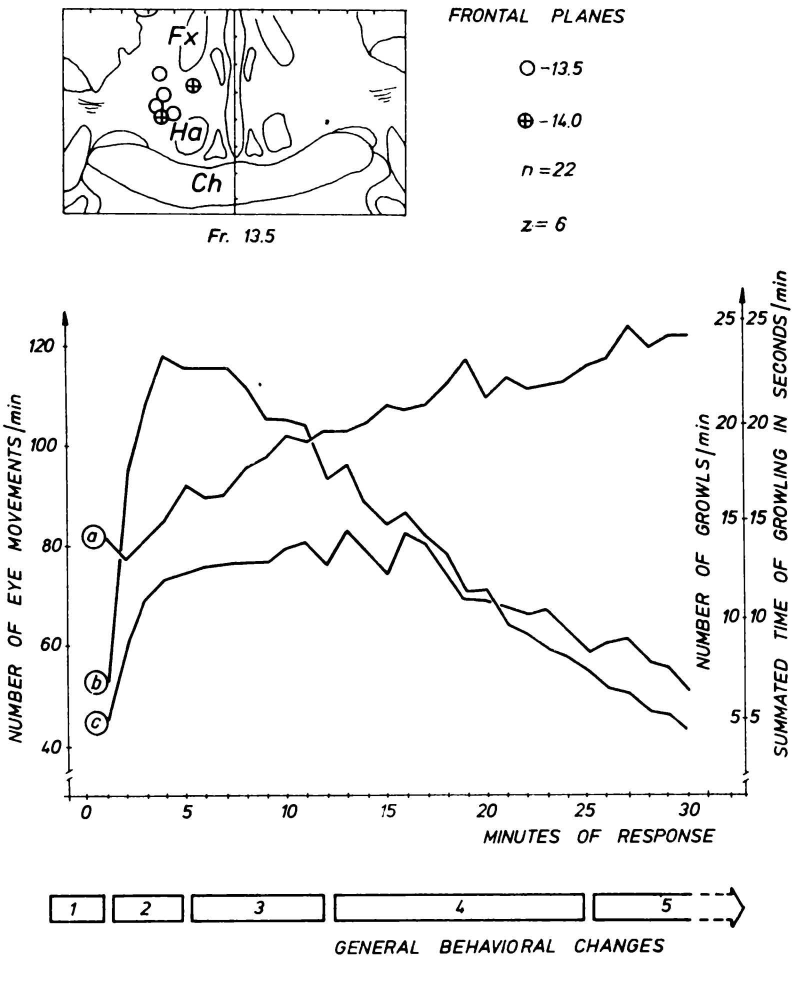

Fig. 7. Comparison of time-courses of eye movements (a), vocalization (time of growling (b) and number of growls (c)) and general behavioral changes (bottom of the Figure) from the same responses induced by unilateral intrahypothalamic injection of CCh (10 μg). General behavioral changes consisted of the following stages: 1, latency period similar to pre-injection state; 2, violent development of agonistic attitude; 3, plateau of the full-blown response, growling occasionally accompanied by hissing; 4, evident decrease of agonistic attitude and weak locomotion appearing in 13.7% of sessions; 5, further subsiding of response, in 22.7% of sessions animals came to the window and tried to get out of the chamber. Other denotations as in Fig. 2. See text for statistical evaluation.

DISCUSSION

Gross behavioral changes are the essential feature of the emotional-defensive response induced by intrahypothalamic microinjections of CCh. The cats changed their attitude towards environmental cues after injection and they started to treat a lot of neutral and even attractive stimuli as aversive ones (11). The present findings indicate that for qualitative and quantitative determination of the above described response vocalization is a more useful and adequate parameter than eye movements. The vocalization changes reflected both the level of the response and its time-course while eye movements were of quite different characteristic.

Simultaneous recordings of eye movement numbers and vocalization enabled us to divide the obtained response into two phases: (i) violent increase of all recorded parameters, and (ii) subsiding of aversive arousal and vocalization while general excitement persists. These two phases of the CCh-induced response were noticed in earlier investigations (20), in which it was additionally stated that such correlates of the response as blood pressure and heart rate persisted at high level (after the initial strong increase) and even indicated the tendency to a further increase during the second phase of the response, between the 30th and 60th min after injection. Thus the blood pressure and heart rate values reached their maximum when the emotional-defensive behavior was clearly declining and even approximated the cats' state before injection. Thereby, blood pressure and heart rate changes which accompanied the CCh-induced response were not parallel to behavioral changes. Other investigation (13) demonstrated, that after intraventricular application of appropriate CCh dose the cardio-vascular effects could be obtained without affecting the behavior.

Cardio-vascular changes are commonly regarded as concomitants of emotions (6 p. 49–50, 17, 21, 28, 31). Especially changes of blood flow in limb muscles are considered to be a sensitive and specific index of defensive reaction or emotional stress (1, 2, 12, 21). According to our view, the cardio-vascular changes in cats do not correspond to emotional responses as accurately as CCh-induced vocalization. The cardio-vascular changes in cats during the preparation for fighting were different from those during the fighting behavior (3, 4, 5). Some of the measured values, like heart rate and cardiac output, had even opposite course during these two stages of emotional behavior (3, 4, 5). In a fighting situation the blood flow of limb muscles strongly depended on the cats' position during the fighting (7, 31). In comparison with a natural defence response, cardio-vascular changes obtained by electrostimulation of unanaesthetized animals raise some "doubt on the behavioral significance of the hypothalamic cardiovascular pattern" (31, p. 235).

The changes of blood pressure evoked by intracranial injections of cholinergic drugs provided some additional problems. The fact that intracerebral injections of CCh elicited both rise and fall of blood pressure (9, 10) from some points of rat hypothalamus, and that centrally applied d-tubocurarine, inducing a behavioral response opposite to CCh (15, 25), led to a similar blood pressure increase (18, 26, 27), raised doubts if the obtained cardio-vascular changes presented an independent response of pressive elements, or if they reflected an integrative capacity of the hypothalamus (23, p. 82).

Among the correlates of the emotional-defensive state measured in the present investigation, growling appeared to be a specific vocalization form involved in this state. Such vocalization form was never observed without an emotional excitement, at least at the level of anterior hypothalamus and preoptic area (11), The measurements of different parameters of growling showed that the sums of growling time reflected both the intensity of the evoked response and its time-course dynamics. The changes of growling time paralleled the development and the subsiding of defensive behavior, while the changes of eye movements indicated rather a general arousal than the course of agonistic attitude. The changes of the minute sums of growling time did not exhibit any significant correlation with the changes of eye movements. The number of growls measured during the same time intervals did not illustrate the dynamics of response and it was correlated with the changes of eye movements at a high level of significance. All results indicate that the number of growls is related to both general and defensive excitement states.

The hissing component appeared to be useless for quantitative determination of the response, probably due to its great dependence upon the environmental stimuli and a low percentage of spontaneous appearance.

The presented results led to the conclusion that growling (duration of its episodes) in the emotional-defensive response induced by intrahypothalamic CCh application was (i) a specific form of vocalization for the obtained response; (ii) a quantitative index of response intensity and (iii) a value illustrating the dynamics of the time-course of the emotional response.

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