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LATERAL GENICULATE UNIT ACTIVITY IN FREELY MOVING RATS. I. RELATION TO BEHAVIOR AND STIMULUS RELEVANCE

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Abstract. Using semimicroelectrodes implanted in the dorsal lateral geniculate body unit responses to light stimuli were recorded in two groups of rats in the state of water deprivation and after satiation. The animals of one group were trained to keep still in order to receive water, the others were trained to approach water dispenser on the light stimulation with a water reward. Responses of about two thirds of the units recorded in both groups differ depending on the animals' behavior or motivational state. Drinking before stimulation had little influence. In spite of a similarity of behavior in both groups there was a significant tendency only in the LT-group, consisting of a prolongation of the postexcitatory suppression periods and an increase of the second excitation in satiated animals vs. water deprived ones. This might be ascribed to processes connected with the biological meaning of the light stimulus.

INTRODUCTION

In former experiments (2) in which a comparison was made between responses of lateral geniculate body (LGB) neurons to light stimuli recorded in water deprived and in satiated animals it was demonstrated that differences of unit discharges at high significance level ($P \leqslant 0.001$)

occurred in one third of the units when light was a conditioned stimulus followed by a behavioral reaction of the thirst-motivated rat. In control animals to which the light stimulus had no biological meaning, only minor differences ($P \leqslant 0.05$) could be observed.

Although the light stimuli were delivered during periods of motionlessness, the behavior of the trained vs. untrained rats differed during the experimental session. After habituation, untrained rats were commonly in a state of relaxed wakefulness even during water deprivation. Thirsty trained rats sat in a tonic posture, their head erected when light stimulation was applied. During the interstimulus interval the individuals differed in their behavior going from motionless sitting to vigorous ambulatory movements. As was demonstrated (18, 24) a correlation exists both between unit activity and motor behavior as well as with the state of arousal; this could be scaled to some extent by monitoring the behavior. The question arises whether our previous results were affected by these influences.

When comparing the control and the trained group a second question emerges which deals with the influence of the water reward per se on the unit activity. When their reactions were correct, trained motivated rats were water rewarded after every stimulus. Untrained rats never received water during the interstimulus interval (2).

METHODS

The experiments were performed on male adult albino rats. Two groups of rats deprived of water for 23 h were used. Prior to the recording session each animal was trained to remain motionless in a certain self-selected posture in order to obtain water. Most frequently the rats stood in front of the water spout, at a distance of about 5 cm, the head slightly elevated. After holding this posture for about 5 s the rats of the first group received water immediately through a tube that moved into the box (water trained group = WT). The animals of the second group were stimulated with light and received the reward only when they approached the site where the tube was to emerge within 2 s (light trained group = LT). After the reward a pause of 20 s was interposed during which even the usual posture was not rewarded. The total interval period depended on the further behavior of the animal; the procedure could thus be described as a variable interval reinforcement schedule.

With ether anesthesia, two recording electrodes (insulated NiCr-wires, 50 μm Ø, assembled in bundles of 3 to 5, attached to a plug and cut by scissors (13, 21), impedance 0.5 MΩ at 1000 Hz) were implanted

under electrophysiological control into both lateral geniculate bodies. When spike potentials of stable amplitude could be recorded for about 5 min through one of the wires of the assembly, and a response to light stimulation was present, the skull hole was covered with dental phosphate. Then the plug was fastened to the skull by means of acrylic resin together with a holder for the light emitting diode (LED). An epidural screw on the frontal cortex was used as reference electrode.

The rats were allowed to recover from surgery for three days. Before the recording procedure a cable with the FET-amplifier was attached to the plug. When discernible spikes were detected, the recording session was started in the darkened room after an adaptation period of 30 min. The LED (Fairchild Semiconductor FVL 352) was fastened on in order to stimulate the eye contralaterally to the side recorded. Light stimuli (7 mcd, 560 nm, 15 ms) diffusely illuminating the whole eye were delivered by hand at intervals of 10 to 90 s. Water deprived rats of the light trained group (LT) were stimulated and rewarded in the same way as during the training procedure (D_{rew}). The water trained animals (WT) were stimulated first during a habituation period without water delivery (D) and afterwards randomly during the motionless expectation periods (D_w). Concerning the temporal relation of light stimulation to drinking the following differentiation was established. $D_w a$: unit responses to light stimuli which were delivered after drinking, and $D_w b$: light stimulation after an interstimulus interval without reward. After satiation (S), when drinking behavior was absent, light stimulation was continued. In order to evaluate the influence of general behavioral factors and movements, the behavior of the animals was classified into several types. Two states were differentiated in relation to the behavior at light stimulation, i.e., during the time when unit activity was recorded for compiling the peristimulus histograms. The two states are: motionless sitting, with a lowered or elevated head (usual event, not designated in the Figures) and movements (designated in the Figures by M = head movement, rearing, slow locomotion). As to the behavior during the interstimulus interval (D, $D_w b$, S) respectively after drinking ($D_w a$, D_{rew}) until the next expectatory body posture five stages were distinguished: (i) no movement, (ii) slow movements of the head, (iii) slow exploratory movements, (iv) vigorous ambulatory movements, (v) grooming behavior. These behavioral stages were not seen in all animals, therefore not all units could be included in the full classification program.

The recording technique and other experimental conditions were the same as described before (2). The unit potentials and field potentials recorded with the same electrode were stored on magnetic tape and

analyzed off-line. According to the different experimental conditions and depending on the behavior of each rat PSHs of 256 bins 5 ms each were computed after discrimination of the potentials by means of a window discriminator. The multi-channel analyzer NTA 1024 (EMG Hungary) was used in combination with the EMG 666 computer. To prove the stability of records the unit potentials were superimposed by means of a storage oscilloscope and photographed. Commonly the first 75 ms (15 channels) of the PSH before light stimulation were used to assess the background activity under all conditions. In some cases the background unit activity was evaluated from records without light stimulation at the beginning and the end of the experiment during the thirsty and satiated states. The statistical significance of the responses and the differences between the PSHs under various conditions were evaluated using the χ^2-test with the Yates-correction (9). By means of the test the relative frequency of every bin (number of impulses (m)/number of single trials (n)) was compared with the mean background frequency (R = response significance), and two PSHs derived from the activity of one cell were compared bin by bin (CR = compared responses) (Fig. 1). Due to the low background activity, suppression rarely reached a significant level, when each bin was tested. Therefore sequences of bins with values below the mean background were sum-

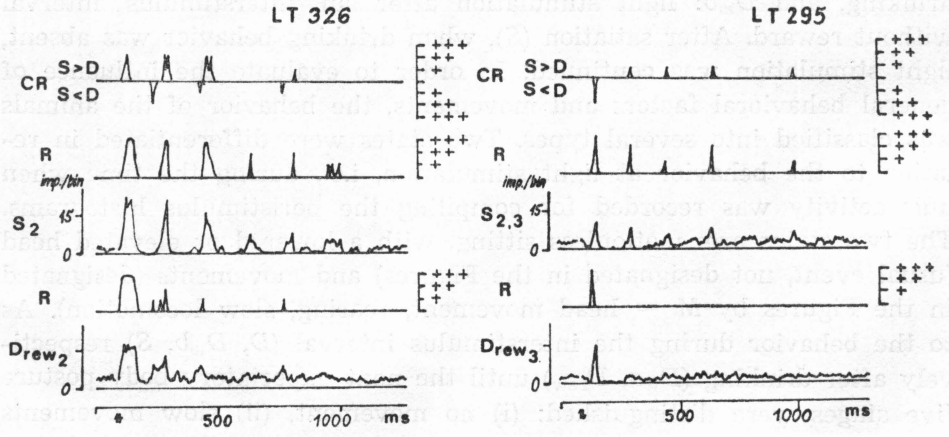

Fig. 1. PSH of the activity of 2 LGB units recorded in the deprived (D) and satiated (S) state of the rat. LT 326: n = 13, LT 295: n = 14, bin width 5 ms. R, significance of exicitatory response phases, above the corresponding PSH: CR; comparison of PSH. (From X–Y-writings controlled by printed values). $+P \leqslant 0.05$, $++P \leqslant 0.01$, $+++P \leqslant 0.001$. D_{rew}, deprived, reaction of the rat to light rewarded by water, *2*, head movement during interstimulus interval, *3*, locomotion during interstimulus interval, *2*, *3*, composed of both behaviors. Arrows: beginning and termination of the light stimulus.

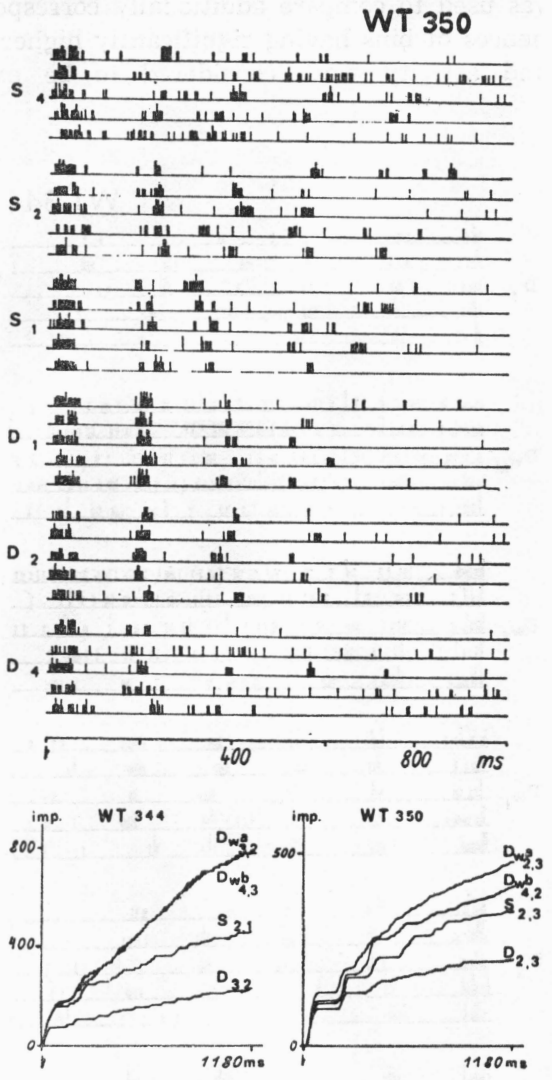

Fig. 2. Single responses of a LGB unit, bin width 2 ms. Below cumulative histograms (integrated PSHs of 10 single responses of two LGB units, bin width 5 ms). *D*, deprived, no water, $D_w a$, light stimulation after water reward, $D_w b$, light stimulation after an interstimulus interval without reward and drinking behavior, *1*, no movement during the interstimulus interval as well as during light stimulation, *4*, vigorous movements during the interstimulus interval. Composed numerals: behavior corresponding denotations. Arrow: termination of the light stimulus. Further denotations as in Fig. 1.

marized to verify phases of suppressed activity with the χ^2-test. The same method was used to compare additionally corresponding phases of two PSHs. Sequences of bins having significantly higher values than the mean background activity were considered to be excitatory phases (Fig. 1).

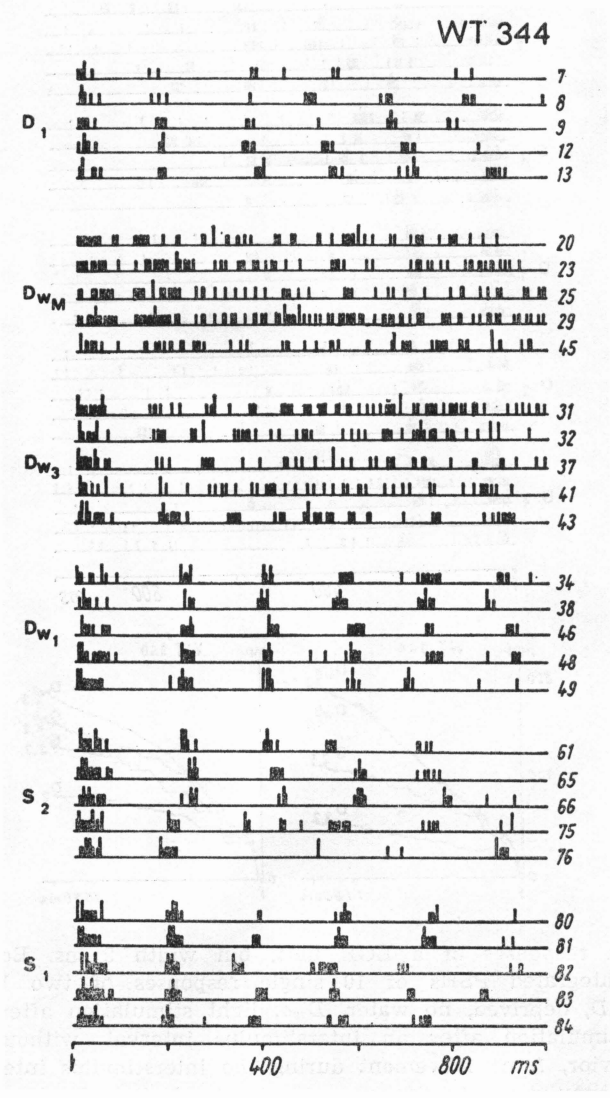

Fig. 3. Single responses of a LGB unit. D_w, deprived, light stimulus given randomly between water reward, M, light stimulation during movement. Numbers at the right side: the number of light responses during the experiment. Further denotations as in Fig. 1 and 2.

To prove significant differences between both groups of animals (WT, LT) the Wilcoxon-test was used (9). Pairs of the following parameters from the PSHs were tested: mean background activity, latency of the first excitatory period (time between onset of light stimulation and the first significant deviation, it is a rough value due to the 5 ms bins), latency and number of impulses of the summit bins of the first and second (if it exists) excitatory phases (bin with the highest value), duration of response phases (first and second excitation, first and second postexcitatory suppression), total number of impulses in a response phase and mean value (number of impulses/number of bins). Furthermore the impulses within a PSH were integrated to a cumulative histogram (CH) (Fig. 2) and the sums compared. Figure 3 shows single responses in oder to underline the results; the PSHs were drawn corresponding to the printed values, sometimes two bins being summed (bin width 10 ms). After ending the whole experimental program electrolytical coagulation was performed for histological control of electrode placement.

RESULTS

127 rats were used. The neuronal activity of 37 animals (20 LT, 17 WT) was appropriate for statistical evaluation. Often it was difficult to discriminate spikes from a single neuron. Therefore the activities of two, sometimes of three cells, judged by their superimposed wave forms, were registered. For the sake of simplicity, the term "unit" is used throughout the paper.

To evaluate the influence of stimulus relevance and motivation on LGB unit responses we tried to summarize single unit responses recorded during similar behavioral acts of the rat. In some cases composing the PSHs from responses during different behavior could not be avoided (Fig. 1, Fig. 2 CH). Comparing the PSHs compiled from unit responses recorded during the deprived state and after satiation in a small number of units we found no changes in their responses (4 LT, 5 WT). As to the degree of significant response alterations of the other units there is a difference between the LT and WT groups. Whereas in WT-unit responses the changes were predominantly limited to a few channels in the PSH, the number of significant response phases being equal in the thirsty as well as in the satiated state, in about half the LT-units some phases were missing when the responses were recorded from thirsty animals (Fig. 1, Fig. 4 LT 311). This means that the results are similar to those mentioned in the already published paper (2). By analyzing the differences between parameters derived from PSHs (see

methods) in group WT (comparison D/S and $D_w a$ or $D_w b/S$) and LT (D_{rew}/S) by means of the Wilcoxon-test the following results were obtained. In the WT-group no statistically significant tendency of the occurring changes was observed. In unit responses of the LT-group there was a statistically significant tendency ($P \leqslant 0.05$) towards a prolongation of the first postexcitatory suppression period in satiated animals as compared to deprived ones. The mean number of impulses of the first as well as of the second (9 cells) suppression period is smaller in satiated animals. The peak of the first excitatory phase occurred in satiated animals one bin (5 ms) later than in deprived ones. The mean number of impulses of the second excitatory period was higher in satiated animals. No statistically significant value could be obtained for the remaining parameters. Summarizing we can state: although the behavior of WT-animals during the period of water delivery (D_w) resembles that of rats trained to react to light stimulation (D_{rew}) statistically significant differences of unit responses are observed only in

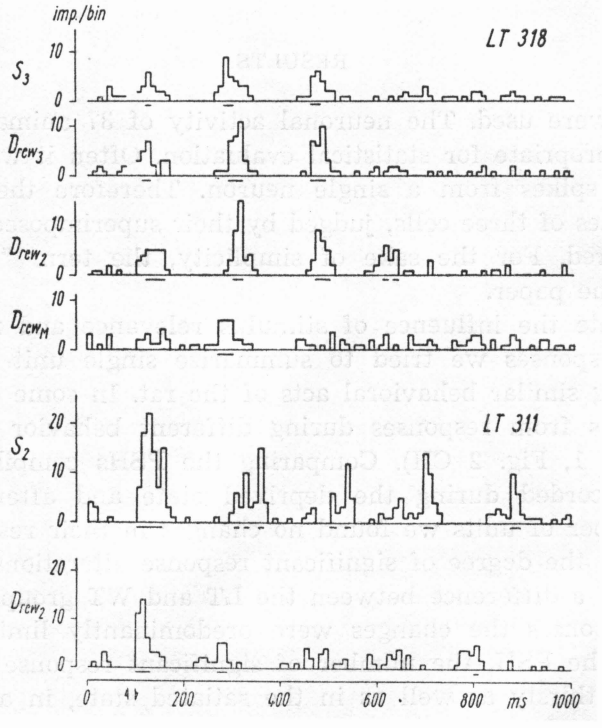

Fig. 4. PSH of the activity of 2 LGB units recorded in the deprived (D) and satiated (S) state of the rat, bin width 10 ms, $n = 10$. Underlined: channels which differ significantly in their number of impulses from the background activity. Further denotations as in Fig. 1 and 3.

the LT-group. When PSHs compiled from responses recorded under the same motivational states were compared in relation to the behavior during the interstimulus interval (Fig. 2, WT 350 *D* 1/4, S 1/4; Fig. 3, WT 344 D_w 1/3, *S* 1/2; Fig. 4, LT 318 D_{rew} 2/3) we could state that in 10 out of 18 units (11 WT, 7 LT) response alterations to light stimuli occurred. Two out of these 10 units were so-called stable ones (2) in relation to the comparison deprived/satiated. 3 out of the 8 units, the activity of which seemingly did not depend on behavioral influences, had modified responses according to the motivational state. With regard to movement during light stimulation (*M*), no different responses could be observed in 5 units. Examples of different responses are shown in Fig. 3 and 4. As already mentioned, such unit responses were excluded from evaluation in the *D*/*S* comparison. Behavior influenced background activity and responses sometimes in different ways.

Analyzing the slow wave activity, we established that there is some relation between evoked potentials and unit activity (3). As far as the EEG is concerned, differences analogous to those observed in the study of unit activity have not been found. During water-deprived as well as during satiated states a basic rhythm of 4–7 c/s predominates in all animals including periods of 15–20 c/s activity mainly in deprived animals. To analyze the influence of the water reward per se in rats of the WT-group unit responses either to light stimuli which were delivered after reward and drinking ($D_w a$) or to stimuli given after an interstimulus interval without reward ($D_w b$) were compared. The responses of 4 out of 14 units showed an alteration (Fig. 2 CH, WT 350). Applying the Wilcoxon test to all the mentioned parameters, no statistically significant value was observed. This means that reward per se has only a minor influence on the responses.

DISCUSSION

Summarizing the main findings we can state: responses to light stimuli of a LGB unit are not only influenced by motivational excitation but also by the level of arousal of the rat, expressed by its motor behavior during the interstimulus interval. Drinking before stimulation has a comparatively small influence. Only in the group of animals where the light stimulus could have a biological meaning there is a statistically significant tendency of changes of unit responses, recorded in the deprived vs. satiated states. Since the behavior of these rats resembles that of a control group, one may assume that neuronal activities due to conditioned reflex excitations are decisive.

It is well established that conditioning leads to different or to new

responses in various brain structures (7, 8, 11, 15, 22, 25) including changed relationships among brain centres (16, 17). In connection with the experimental conditions, both groups of rats (LT and WT) are in expectancy of reward and behave in a manner attributed to operant conditioning. Therefore in both groups differences occur in the excitability of structures within the motor system, depending on the motivational state (deprived or satiated) (29). The reactivity of the thirst-motivated animals to various stimuli is increased (5). The relation of unit activity of LGB and midbrain reticular formation to motor behavior was analyzed by Schwartzbaum (24).

Influence due to water deprivation, i.e., changes in plasma osmolarity, and in hormonal levels (1, 4, 6, 14) leading to neural excitations of hypothalamic and other brain sites (28) would be effective in all groups of animals independently from the training conditions. The focal EEG does not give any hint of differences between both groups.

In other words, additional factors should be included. In the light trained group expectancy of visual stimuli and greater visual attention could increase the degree of excitation in fronto-limbic and visual structures (19, 23, 27). Because in some WT and LT units the changes resemble each other, one may assume that the terminal pathways for excitations reaching the LGB are identical in both groups. As already discussed in earlier papers (2) a disinhibition of the LGB relay neurons via the nucleus reticularis thalami (20) or intrageniculate interneurons (26) would be a plausible explanation of the observed differences, leading mostly to a decrease of inhibitory phases in the motivated animal. Together with the inhibition of neurons of the nucleus reticularis thalami, which could be of cholinergic nature (10), the relay channels through the LGB become uncoupled as suggested by Singer (26). Therefore in the majority of LGB neurons, the discharge synchronizations which occur frequently in the animal's satiated state became less dominant when the animal is thirsty and behaviorally active, in expectancy of the reward. These mechanisms of disinhibition of LGB neurons are discussed as important for improved visual discrimination (12).

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