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Study of the Action of the Nucleus Accumbens Septi Electrical Stimulation upon the Unitary Activity of the Amygdaloid Complex of Waking Cats *

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The extracellular activity of the amygdaloid cells and the action of the NAS stimulation upon them were studied in unanesthetized, non-paralized, waking cats. The neurons were classified according to their responsiveness to olfactory, auditive, visual and behavioural stimuli, and then, the action of the NAS electrical stimulation upon the spontaneous activity of the previously classified cells was studied.

The number of cells responding to visual stimuli (projected spot of light, movement) was found to be higher than in previous works. On the other hand, some of the cells activated by behavioural stimulation (presence of rat) behave in a complex manner by changing the characteristics of the response upon modification of its distance from the rat. However the majority of the recorded neurons failed to respond to any of the tested natural stimuli. The existence of rather extensive zones in the amygdaloid complex without spontaneous activity as well as the small number of cells showing modifications of the rate of firing induced by NAS electrical stimulation was remarkable.

In previous studies (1, 30) it was found that simultaneous stimulation of the Nucleus Accumbens Septi (NAS), Septum or the Head of the Caudate Nucleus and corticomedial complex or area amygdaloidea anterior provoked an inhibition of motor and behavioural responses induced by individual stimulation of corticomedial complex and amygdaloidea anterior area. Inhibition of electrocardiographic responses induced by stimulation of amygdaloidea anterior area and the anterior part of nucleus centralis was also observed

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upon concurrent stimulation of the septum.

This inhibition migth take place either on certain amygdaloid neurons or on other CNS points.

Unitary recordings of some amygdalar neurons (35) showed discharge modifications induced by septum stimulation but no identification of those cells was made in terms of the response to natural (auditive, visual, etc.) stimulations.

The aim of this work is twofold. First, to know what kind of neurons (in terms of its driving stimuli) modified its discharge following NAS stimulation, and second if this modification of the firing rate might explain the inhibition of agonistic, behavioural, and electrocardiographic responses founded by paired NAS and amygdaloid stimulation (1). To test this, extracellular activity of amygdalar neurons in wake cats was recorded and a classification in different groups was made on the basis of their responses to auditory, olfactory, somesthesic, visual and behavioural stimuli. Then, the effect of NAS electrical stimulation upon the spontaneous neuronal discharge was studied in each group.

Materials and Methods

Experiments were performed on 11 adult cats, of both sexes, weighing 2-3 kg. All cats, preoperatively selected, did attack rats spontaneously. Each animal was anesthetized with nembutal 40 mg/kg i.p., and placed in a stereotaxic instrument. Under aseptic conditions, the fur of the skull was incised, and a hole was opened in the bone over the stereotaxic coordinates of the amygdaloid complex. A stainless steel cylinder 2 cm in diameter was vertically oriented on the hole, its center at stereotaxic coordinates AP + 10, LAT + 10 according to SNIDER and NIEMER's atlas (31). The cylinder was fixed to the bone with dental acrylic, and served as a pedestal for a hydraulically operated microdrive which allowed multiple penetrations in stereotaxic selected locations.

Two silver-chloride electrodes were situated in the external orbital rims to record the horizontal electrooculogram (EOG). In addition, two stainless steel screws were implanted in the skull for electroencephalographic (EEG) monitoring. A bipolar nichrome electrode was stereotaxically placed in the Nucleus Accumbens Septi (NAS). The leads were brought subcutaneously to a small plug fixed to the skull with dental acrylic.

Following surgery the cats were left in their cages for two days with food and water *ad libitum*. Recording sessions began on the 3rd day. During the experiments the cat's head was attached to a frame by means of two transversal bars fixed to the bone with dental acrylic. This unpainful procedure allowed the cat some body movements and free movements of the forelimbs. At the end of each session the cat was returned to its cage, with food and water, until the next day. Daily i.m. antibiotics were given.

For recording glass insulated platinum-iridium microelectrodes with an impedance of between 2-3 megaohms were used.

After each penetration was completed two electrolytic lesions were made: at the end and at the beginning of the tract of the amygdala penetration, passing 10 μA direct current for 10 s.

Electrical activity at the microelectrode tip was passed through a Grass High Impedance Probe (mod. HIP 511E) and a Grass (P511) preamplifier. The amplified signal was fed through a high pass filter and displayed in a Tektronix oscilloscope. A Differential Amplitude Discriminator (DAD) was used. The EOG, EEG and DAD output were monitorized in a Reega-VIII poligraph. The DAD output was fed to a Tektronix memory scope and displayed as dots, each dot being a spike. A row of dots (spikes) from left to right is a raster; 32 rasters, from below to above were generated, the time base being 1 cm/s (10 s each raster). A Grass P88

stimulator, and a Tektronix 2620 stimulus isolator were used for NAS electrical stimulation. Bipolar pulses of 1 ms of duration and a frequency of 100/s for 200 ms were used. The amount of recurrent used was always subthreshold, i.e.; below the threshold necessary to evoke a NAS motor response.

Rough data and DAD output were stored in an Ampex magnetic tape for posterior analysis. A multi-scale program of an Elatron 1600 lab computer was used to make frequency/time histograms.

When a distinct unitary activity was isolated in the DAD a systematic exploration was completed: 1) somesthetic stimulation: gentle skin stimulation, passive joint movements, and muscle palpation; 2) olfactory stimulation: induced by the smell of a box with a mouse inside but out of the cat's view, or by cigarette smoke; 3) auditory stimulation: meowing, barking, taped singing birds, whistling, and tapping a table; 4) visual and behavioural stimulation: (a) projecting a spot of light on a screen or the movements of any object in front of the cat's view; (b) the experimenter threatened the cat (who responded with one or several of the following components: flattening the ears, an intent of withdrawal of the body, puffs, strokes with a paw); (c) a rat was held in front of the cat's view out of his paw's reach. Sometimes the cat was allowed to catch the rat with his fore paws.

On the above basis, a neuron was classified into one of the following two groups: 1) those cells not driven by any of the conditions listed above, we call them Non Driven cells (ND), and 2) those cells driven by one or several of the above explorations, we call them Driven cells (D). Several subgroups of the D cells are made on the basis of their driving stimuli. The action of the electrical stimulation of the NAS was studied both in ND and D neurons.

When the study was finished, the cat

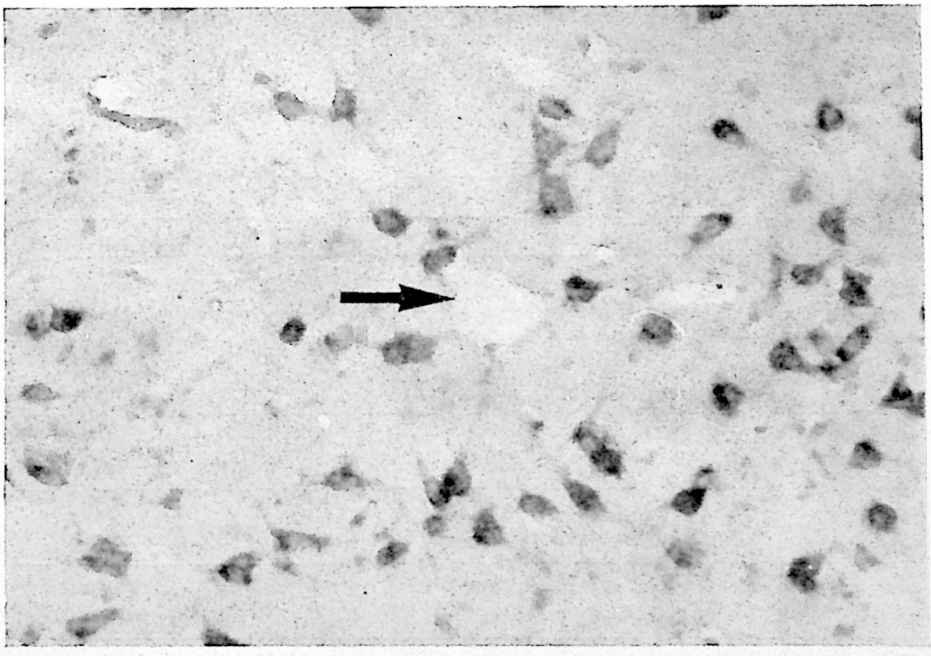

Fig. 1. *Small electrolytic lesion in n. lateralis.*

was anesthetized with nembutal, i-p., and its brain was perfused, first with saline, and then with formaline 10 %. The brain was cut at 20 microns sections, and stained with toluidine blue (fig. 1).

Results

By means of 85 microelectrode penetrations with tracts identified histologically in the different amygdalar nuclei, 666 neurons were studied. In table I the distribution of the ND and D neurons in the different amygdala nuclei can be found.

In the amygdala most neurons are ND: 500 out of the 666 (75.08 %). The spontaneous discharge frequency of the ND neurons oscillates between 1-14/second with the maximal peak at 4/second. None of the exploratory stimuli utilized, isolated of in combination, modified the spontaneous discharge frequency of this neuronal group.

The electrical stimulation of the NAS caused modifications in the spontaneous discharge rate in some of the neurons of both the ND and D group (table I), but no significant statistical differences between ND and D group were found with the Student's test.

The characteristics of the inhibitory and excitatory actions of the NAS stimulation are identical for both the ND and D groups. The inhibition or excitation of the amygdalar neurons spontaneous discharge exceeds the stimulation time of the NAS (fig. 2); the duration of the inhibition or excitation being directly related to the intensity of the stimulation: the greater the intensity of the stimulation the greater the time of inhibition or excitation. The recuperation time of the prestimulus frequency of discharge is variable, but it depends also on the intensity of the stimulus used. Neurons were classified as inhibited or excited by stimulation of the NAS if the prestimulus discharge frequency was recuperated after the end of the stimulation period. The observation time for the recuperation of the prestimulus frequency, was arbitrarily set to the same time in which the neuron had been study during the stimulation of the NAS. This time oscillated between 2.5 and 5 minutes.

Table I. *Nuclear distribution of ND and D neurons, and the effect of NAS stimulation.*

		NAS electrical stimulation				NAS electrical stimulation		
Nucleus	ND neurons	Increase	Decrease	No effect	D neurons	Decrease	Increase	No effect
Central	158	9 (5.70 %)	8 (5.06 %)	141 (89.24 %)	54	4 (7.41 %)	4 (7.41 %)	46 (85.19 %)
Basal	112	4 (3.57 %)	13 (11.61 %)	95 (84.82 %)	38	3 (7.89 %)	0 (0 %)	35 (92.11 %)
Lateral	89	4 (4.49 %)	8 (8.99 %)	77 (86.52 %)	43	3 (6.98 %)	2 (4.65 %)	38 (88.37 %)
Medial	137	6 (4.38 %)	15 (10.95 %)	116 (84.67 %)	31	3 (9.68 %)	3 (9.68 %)	25 (80.65 %)
Cortical	4	0 (0 %)	0 (0 %)	4 (100 %)	0	0 (0 %)	0 (0 %)	0 (0 %)
TOTAL	500	23 (4.60 %)	44 (8.80 %)	433 (86.60 %)	166	13 (7.83 %)	9 (5.42 %)	144 (86.75 %)

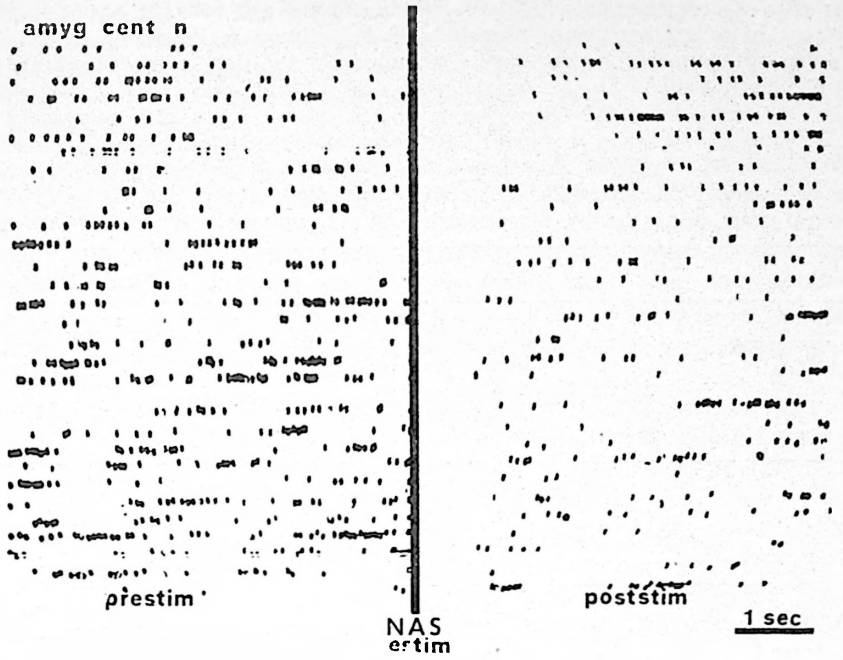

Fig. 2. *ND neuron of the central n.*
Each dot corresponds to a spike; a row of dots from left to right is a «raster», and 32 rasters are generated from below to above. The duration of each raster is of 10 sec. The first 5 seconds correspond to the prestimulus (prestim), at the 5th second NAS is stimulated for 250 msec (see Methods) (NAS estim). The NAS stimulation induced an inhibition of the discharge for one sec.

The neurons that underwent a modification of their discharge by the stimulation of the NAS, were found in both the ND and D groups. Within group D there was no subgroup in which the inhibitory or facilitatory action predominated (except in the D group of Basal n) nor any special anatomical distribution of the neurons affected by NAS stimulation.

There are no significant statistical differences between the number of amygdalar neurons which increase, decrease or whose discharge is not affected by stimulation of the NAS.

Only 166 neurons of the total 666 (24 : 92 %) were classified as D by the criteria outlined above. This neuronal group, except for the cortical n, extends to all the amygdalar nuclei. Its spontaneous discharge frequency oscillated between 0 and 14 per second, with a greater number of neurons discharging at 4 per second. All of the D neurons have a spontaneous discharge in absence of stimulation except for some neurons responding to auditive stimulus.

Table II presents a summary of the response of D neurons to tactile, olfactory, auditive, visual and behavioural stimulus, and the action of the NAS stimulation upon them.

Tactil stimulation. Of the 166 D neurons, 10 increased their frequency by gently stimulating the skin. The receptor fields were large and more frequently covered the contralateral face and neck, fore limbs, and neck or the back (table II).

Table II. *Nuclear distribution of D classified neurons and effects of NAS stimulation.* Each column shows the number of neurons and the induced modifications of the basal rate by the tactile, olfactory, etc., exploratory stimulation. At the right of each column the action of the NAS stimulation upon the spontaneous rate of each previously classified neuron is shown; i.e.: in the column labeled «visual», in the central n. 18 cells increasing the firing rate and 2 decreasing it when a spot of light is projected or some object is moved in front of the cat's view. The right column shows that 14 cells out of the 18 do not change their discharge following NAS stimulation; 2 cells increasing it and 2 decreasing it. The 2 cells that decrease their discharge by visual stimulation do not change it by NAS stimulation.

Nucleus	Tactile	NAS	Olfactory	NAS	Auditive	NAS	Visual	NAS	Visual threats	NAS	Rat	NAS	Total
Central	7+	7 O			6+	6 O	18+	14 O 2— 2+	8+	1 O 7+	8+	8 O	54
							2—	2 O	1 O	1 O	3— 1 *	3 O 1—	
Medial			1—	1 O	6+ 1—	5 O 1— 1 O	11+	9 O 2+	3+	3 O	4+ 5—	3 O 1+ 4 O 1—	31
Basal					11+ 2—	9 O 2+ 2 O	13+	13 O			4+ 5— 3 *	3 O 1+ 5 O 3 O	38
Lateral	3+	3 O			3+	3 O	34+	29 O 2— 3+			1+	1 O	43
							2—	2 O					
TOTAL	10	10	1	1	29	29	80	80	12	12	34	34	166

Signs: + for increase; — for decrease; O for no effect; * complex.

Olfactory stimulation. Only one neuron decreased its discharge when the cat smelled cigarette smoke (table II).

Auditive stimulation. Twenty nine neurons responded to some of the complex auditive stimuli described above, more frequently to meowing and barking (table II). The spontaneous discharge frequency of these neurons oscillated between 0-16/s.

Two of the eleven auditory neurons identified in the basal n. were also activated by non-auditive stimuli: one by visual stimuli and the other by the sight of a rat.

No significative anatomical distribution was encountered in the amygdalar nuclei for these 29 auditive neurons.

Visual and Behavioural Stimulation. The types of exploratory stimuli utilized have been described above. We shall classify the neurons in relationship to their response to the three explorations referred to as: (a) visual stimuli, (b) visual threats and (c) rat (see above).

(a) *Visual stimuli:* Eighty neurons activated by a luminous point projected on a screen or by moving objects in front of the cat's visual field were included in this group. This neuronal group habituated

very rapidly, and a change in the direction of the luminous point or object being used was sufficient to make the neuron respond again. Frequently these neurons stopped firing during the exploration and no type of stimulus could make them discharge again. When this occurred before the series of explorations described above could be completed, the neuron was not included in the report. All the neurons included in this group had spontaneous discharge and its frequency increased during the exploration. Table II shows their nuclear distribution and the NAS action upon the spontaneous activity of these cells.

(b) *Visual threats:* Twelve neurons whose discharge was modified by visual threats were identified: 9 in the central nucleus and 3 in the medial nucleus (table II).

These neurons modify their basal discharge frequency with visual threats, which evoked stereotyped patterns of movement in the cat: flattening the ears, an attempt to draw back the body and strokes with a paw. No special anatomical distribution of these neurons was founded.

(c) *Rat:* Thirty four amygdalar neurons modified their spontaneous discharge when the cat saw a rat (table II).

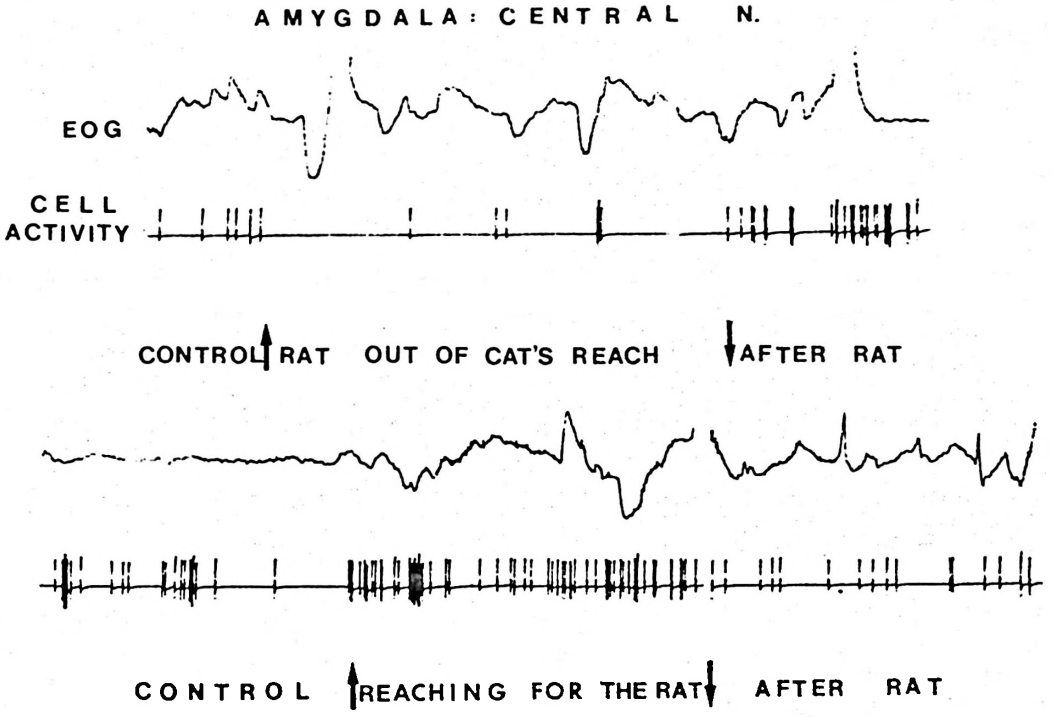

Fig. 3. *Central nucleus.*
Above. Control: spontaneous discharge in absence of stimulus. When a rat is placed in front of the cat but out of reach, discharge frequency diminishes (rat out of cat's reach), to be reestablished when the rat is removed from the cat's field of vision (after rat). Below. The same neuron as above; on placing the rat near the cat, and when the cat catches it with its fore -paws (reaching for the rat) discharge frequency increases, to be reestablished at control levels when the rat is removed from the cat's paws and field of vision (after rat).

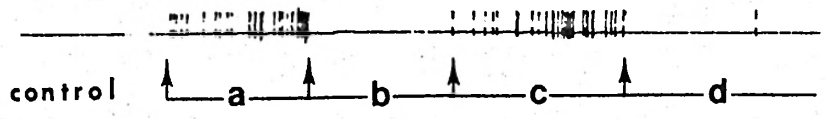

Fig. 4. *Neuron D of the basal nucleus which does not discharge spontaneous (Control). a)* rat in front of cat, but out of reach, producing cellular discharge *b)* rat is moved towards cat, which catches rat between its fore-paws, when neuron discharge ceases; *c)* as a; *d)* as b.

One neuron localized in the central n. behaved in a complex manner: the discharge frequency decreased when the rat was maintained within the cat's vision but out of paws' reach and increased the discharge frequency when the rat was brought forward into the cat's reach (figure 3). Spontaneous discharge of the complex neuron was inhibited by NAS stimulation.

Three of the 12 neurons located in the posterior part of the basal n. were classified as complex. The first increased its spontaneous discharge when a rat was maintained in the cat's field of vision but out of reach, and stopped its discharge when the rat was situated within reach distance and the cat tried to reach the rat (fig. 4). The other two neurons increased their discharge frequency when the rat was captured by the cat. One of these neurons also increased its discharge frequency with auditive stimulation. Stimulation of the NAS did not modify the neuron's discharge.

No special anatomical distribution of these neuronal group was established.

Discussion

Most of the amygdalar neurons did not modify their basal discharge rate (75 % ND) with any of the utilized stimuli. In view of the diverse function of the amygdaloid complex we can suppose that in the cat' normal behavior a complex stimulus or situation should be capable of inducing some change in the activity of this neuronal group. Therefore their classification as ND would be related only to the method utilized here.

We would like to point out to the fact, constantly observed in this work, that the neurons were localized in groups at different levels of the microelectrode path, but that the major part of the microelectrode path is free of activity both spontaneous and evoked by the stimuli utilized. We cannot explain this fact by the different density or neuronal size in the different segments of the microelectrodes path, since, as showed by histological studies, it was about the same as in the zones where a greater activity, spontaneous or evoked, was registered. For the same reason an explanation based on the physical properties of the microelectrode and its position with respect to the neuron (26), cannot be the total explanation. We can thus suspect that in these «silent» zones there are very specific neurons that are only phasically activated.

In accordance with other authors (3, 27, 28) we have confirmed the existence of convergence of different inputs on some of the amygdalar neurons. In thirteen D neurons out of 166, the convergence was encountered with: tactile and visual stimuli in the lateral nucleus. Auditive and visual in the basal nucleus. Auditive and visual (rat) in the basal and medial nuclei.

Only one olfactory neuron was identified, located in the medial nucleus, one of the amygdalar nuclei with olfactory connections (20). This calls attention to the fact that no olfactory neuron was identified in the cortical nucleus, the principal amygdalar nucleus of olfactory projection (20). Some of the olfactory

stimuli used were the same used by other authors (5, 28), but perhaps odours more related with the cat behaviour would be more effective in driving the cells.

The sounds which modify the activity of the auditive neurons are complex: Whistles, meowings, taped birds songs, etc., such as has already been pointed out by other authors (28). Their distribution being greater in the basal nucleus, followed by the medial, central and lateral nuclei.

In contrast with the results of other authors (24, 28) the number of auditive neurons identified was less than the number of visual neurons identified. Although this lesser number of auditory cells may be because the appropriate trigger stimulus (because of its complexity) was not founded. These are neurons that respond to moving objects in front of the cat and habituate easily. The greater number was found in the lateral nucleus, followed by the central, medial and basal nuclei. Such a high number of neurons that respond to visual stimuli can explained some of the symptoms of a Klüver-Bucy Syndrome (10, 14). The destruction of these neurons could be related to visual agnosia or to psychic blindness characteristics of this syndrome, even when the psychic blindness does not appear to be caused by isolated destruction of the amygdala (12).

Twelve neurons, localized in the central and medial n. respond only when threatening gestures were performed by the experimenter in front of the cat. To these «visual threats», cats displayed some of the components of the agonistic reactions that were observed in free cats when defence reactions where elicited by stimulation of the appropriate amygdalar zones (11, 13, 15, 30, 36).

The basal, central and medial nuclei are the amygdalar regions whose stimulation, according to different authors, leads to the defense responses (7, 8, 13, 15, 16, 30, 32, 34, 36) and to components of the defense reactions (4, 19, 21, 23, 25). This takes place especially in the lateral part of the central nucleus and in the basal magnocellular nucleus.

If the neurons described here that respond to threats, are related to the defense reaction or to some of the components that accompany these reactions, it is striking that none have been located in the basal magnocellular nucleus from which the said reactions are more easily evoked; perhaps technical differences, may account for different results.

The firing rate modification of the complex cells that respond to sighting of the rat (figs. 3 and 4), should be a function of significant changes in the stimulus and in the cat's behavior. This implies that a great variety of information, necessary for the manifestation or adaptation in the final behaviour, converges upon the neurons of the amygdala.

Such changes of the neuronal activity in function of the stimulus type (sight of the rat out of the cat's reach and attacking the rat when it is within reach) could be related to the two components of attention and defense of the «defense reaction» (4, 9). In any case it points out the small number of neurons of this type identified.

Lesions of the septal region in rats, mice and cats produce a change in behaviour, which has been described as hyperreactivity (6, 22). TURNER's work (33) showed the importance that the stria terminalis would have in the development of the septal syndrome. In general it is agreed that the adequate place for producing hyperreactivity is in the region ventral to the septum (2), especially the ventral area of the anterior septum including parts of the diagonal band of Broca and the Nucleus Accumbens Septi.

The amygdala would be implicated in these reactions of «septal rage» since the amygdalectomy in rats reduces this syndrome (17, 18, 29). The possibility that the hypothalamus may also be implicated in the septal syndrome is not discarded in

view of the anatomical connections with the region ventral to the septum (2).

The inhibitory action of the NAS (1) or septum (30) stimulation upon the motor (agonistic) and ECG responses induced by stimulation of the corticomedial complex or amygdaloidea anterior area, are readily and consistentely provoked. At unitary level, the NAS stimulation induced changes in activity of neurons located in all amygdaloid nucleus, except the cortical.

The spontaneous discharges of the great majority of the DN and D neurons are not affected by NAS stimulation (table II); there are not significant statistical differences using Student's test between the increasing and decreasing effects of NAS stimulation on ND and D cells. There are also no statistical differences between the increase and the decrease of the spontaneous rate between the D group following NAS stimulation, except for the basal nucleus.

The only cells that increase or decrease their spontaneous discharge by NAS stimulation are the auditive, visual and rat neurons; tactile and olfactory cells are not affected.

On the basis of the preceding results there is not any correlation either of the nucleus and type of neurons affected by the NAS stimulation and the inhibitory effect of the NAS (1) stimulation upon the agonistic and ECG responses elicited by paired, simultaneous stimulation of the corticomedial complex of the amygdala in chronic, freely moving cats.

An explanation for the low number of neurons whose discharge is affected by NAS stimulation could be that the action of the NAS stimulation were tested upon the spontaneous discharge of the neuron, and not when the neuron was driven by its driving stimulus. This was done in this way because of technical limitations. But some neurons, most of them belonging to the «visual» D group could be tested with simultaneous stimulation of NAS and the corresponding natural driving stimulus, the result being the same as the NAS stimulation on the neuron basal discharge. Nevertheless the low quantitative effect of the NAS stimulation at unitary amygdaloid level may not imply a low qualitative effect of the NAS stim on the agonistic and ECG responses of the amygdala in chronic cats.

On the other hand the control of the agonistic activity could be exerted from other structures besides the NAS (1, 30, 33) or upon other structures such as the hypothalamus (2).

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Resumen

Se estudia en gatos despiertos y libres de la acción de relajantes musculares la actividad extracelular en la amígdala y la acción sobre ésta de la estimulación eléctrica del NAS. Las neuronas se clasifican según su respuesta a estímulos olfativos, auditivos, visuales y de conducta y, después, se estudia la acción de la estimulación eléctrica del NAS sobre la descarga espontánea de esas células previamente clasificadas.

Se encuentra un número mayor de células que responden a estímulos visuales (proyección de puntos luminosos sobre una pantalla, movimientos) que en otros trabajos. Por otra parte, algunas células cuya actividad está relacionada con estimulación de conducta (presencia de una rata) se comportan de forma compleja, cambiando las características de la respuesta al modificar la distancia entre la rata y el gato. Sin embargo la mayoría de las neuronas no responden a los estímulos exploratorios. Destaca la existencia en el complejo de la amígdala de zonas más bien extensas sin actividad espontánea, así como el escaso número de células que presentan modificaciones de la frecuencia de descarga inducida por estimulación del NAS.

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