

## SINGLE UNIT RESPONSE TYPES IN THE PULVINAR OF THE CEBUS MONKEY TO MULTISENSORY STIMULATION

RICARDO GATTASS, AGLAI P. B. SOUSA and EDUARDO OSWALDO-CRUZ

*Departamento de Neurobiologia, Instituto de Biofísica, Universidade Federal do Rio de Janeiro Centro de Ciências da Saúde, Bloco G, Cidade Universitária, Ilha do Fundão 20.000 - ZC. 32 Rio de Janeiro (Brasil)*

(Accepted March 16th, 1978)

---

### SUMMARY

Response to sensory stimulation was studied in 162 neurons in the pulvinar of Cebus monkeys in 4 acute and 5 chronic preparations. Two basic response patterns were observed: type I responses, similar to those obtained in primary relay centers, were only observed after visual stimulation. Type II responses were obtained after stimulation of more than one sensory modality. Characteristically these responses presented fatigue and habituation. Temporal relationship between stimulus and response was not as clear as in type I responses, afterdischarge frequently occurred. Taking these response types into consideration two groups of units were identified in the pulvinar. Units of group A (91 neurons) showed type I response to visual stimulation. For these units receptive fields similar to those found in other regions of visual projection could be defined. As a rule units of group A displayed type II responses to other sensory modalities. Units of group B (71) did not display type I responses; they always responded to visual, somatic, auditory and olfactory stimuli with type II responses. They could be activated by a single sensory modality (B, unimodal) or by more than one sensory modality (B, multimodal).

---

### INTRODUCTION

Visual evoked potentials have been reported in the pulvinar of the cat<sup>3,4</sup> and monkey<sup>19</sup>. Single unit studies of this nucleus confirm the presence of visually driven neurons in both species<sup>14,20,25,29</sup>. In addition, multisensory units have been reported in the cat's pulvinar<sup>10,17</sup>, contrasting with the monkey in which only somatically driven units were found<sup>25</sup>. Structural and functional evidence suggests that the pulvinar receives projections from various cortical and subcortical regions which in turn receive visual, somatic and auditory inputs<sup>26,28,31,32</sup>. The influence of other sensory modalities

on visually evoked unitary responses observed during a single unit analysis of the Cebus pulvinar<sup>13</sup> led us to a more detailed study of the multisensory projections to the pulvinar.

#### MATERIAL AND METHODS

A total of 9 adult Cebus monkeys weighing 1.4–3.2 kg were used in acute (4) and chronic (5) preparations. In the acute preparations the animals were sacrificed and perfused at the end of the recording session. In the chronic ones after each recording session the animals were allowed to recover from neuromuscular block, returned to the animal's room and used again after a resting period of 4–10 days. This procedure was adopted after we observed that arousal, as judged by the EEG tracings, could not be promoted after the first day of recording. In all animals a prothesis enabling the orientation of the head in stereotaxic coordinates was implanted onto the skull a few days prior to recording sessions. Surgery and maintenance of the animal have been described in a previous publication<sup>12</sup>.

The acute preparations were initially anesthetized either by an intraperitoneal injection of pentobarbital (30 mg/kg, 3 animals) or by an endovenous injection of Fabantol (Bayer; 20 mg/kg, 1 animal). All chronic preparations were anesthetized by an initial dose of ketamine hydrochloride (Ketalar, Parke Davis, 20 mg/kg). In all cases analgesia was maintained during the recording sessions by a mixture of 70% N<sub>2</sub>O and 30% O<sub>2</sub>. In addition all chronic preparations were sedated by a small dose of diazepam (Valium, Roche, 0.5 mg/kg).

The animal's head was attached to a stereotaxic frame by the previously implanted prothesis while the body rested in a cushioned support. The experiments using acute preparations lasted on the average 38 h. In the chronic experiments 2–9 recording sessions with an average duration of 16 h, were carried out in each animal.

Single unit activity recorded by means of tungsten microelectrodes was amplified and displayed by conventional methods. The discharge from individual neurons was selected by an amplitude discriminator, the output of which was led to a Digital PDP-12 computer for real time on-line processing. A Hewlett-Packard 3520B tape recorder enabled storage of data for off line processing.

Somatic stimulation was carried out directly by the investigator, by stroking or blowing the animal's fur, touching glabrous skin surfaces, moving joints or applying pressure to the body surface. Auditory stimulation was delivered by means of an ear-phone placed in the immediate vicinity of the auditory canal. Auditory stimulation in both acute and chronic preparations was achieved by pure sounds of various frequencies or by a series of clicks as well as by behaviorally meaningful sounds recorded in magnetic tape. Alarm cries, vocalization associated with aggressive behavior or the sound emitted by the rattle of a rattle snake were shown to be more effective in promoting arousal. Olfactory stimulation, used only in acute preparations, was achieved blowing ammonia vapors through the nostrils.

Visual stimulation was carried out by retroprojection of light or dark spots, slits and bars or of other patterned stimuli on a tangent screen placed 57 cm in front of the

animal's eye. The stimulus projecting system could be controlled by the computer enabling on-line correlation between stimuli and cell response. A more detailed account of the hard and software employed is described in another publication<sup>13</sup>.

Spontaneous cell discharge and its alteration resulting from sensory stimulation was analysed on-line by means of a program that displays sequentially the logarithm to the base two of the interspike interval, resulting in a display of interspike interval versus time, similar to that described by Chung et al.<sup>9</sup>. In this type of display each dot denotes the occurrence of an impulse and its vertical displacement gives the duration of the interval, in milliseconds, between the impulse and the preceding one. Because sequential pulse intervals vary widely, from a millisecond to seconds, a logarithmic representation of the ordinate was adopted in order to avoid compression of the short-interspike intervals when displaying long interspike intervals in the same scale.

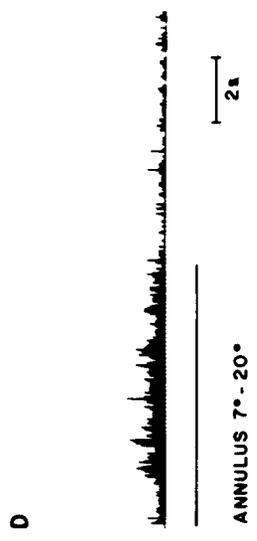
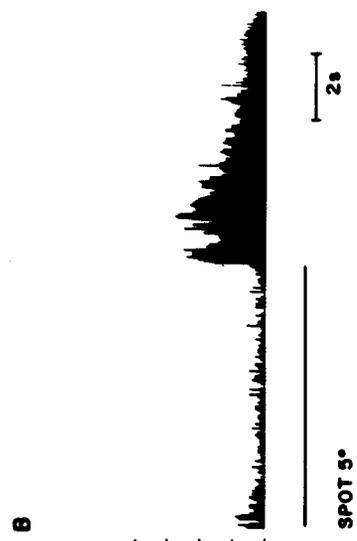
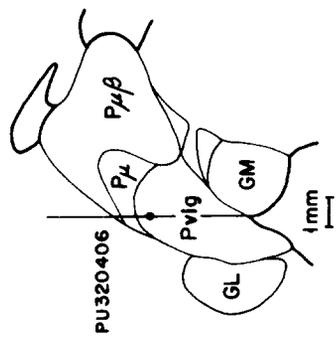
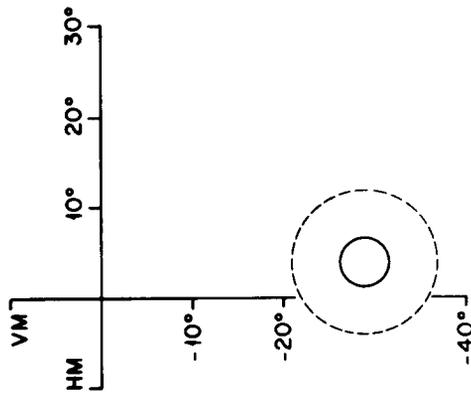
At the end of the last recording session the animals were deeply anesthetized and perfused through the aorta with saline (0.9%) followed by formaline (4%). Following decapitation the head was kept in fixative overnight. Correlation between recording site and cytoarchitectonic subdivisions was achieved by inspection of 40  $\mu\text{m}$  coronal frozen sections stained with cresyl violet. Determination of recording sites was facilitated by performing small electrolytic lesions during the penetrations (5–20  $\mu\text{A}$  for 5–15 sec, tip positive) in both acute and chronic preparations. The small electrolytic lesions and associated glial reactions enabled the identification of individual penetrations carried out with an interval of several days in the chronic preparations.

## RESULTS

A total of 162 units were isolated in the pulvinar of 9 Cebus monkeys. The study of the response of these units to stimuli of various sensory modalities revealed the existence of two distinct types of response. Type I response patterns are similar to those observed in primary relay centers, that is, they show a strict temporal correlation between stimulus and response, and they are able to follow a relatively high frequency of stimulation with little or no habituation. In addition this type of response showed some degree of dependence on the state of arousal. Under adequate conditions of arousal it is possible to define receptive fields that show patterns of organization similar to those reported in various primary relay centers. Responses of type I were only observed following visual stimulation.

A different response pattern, type II, was evoked by this and by other sensory modalities. Correlation between response and stimulus onset and termination is not as clear as in type I. Response intensity could show a gradual increase after the onset of stimulation and, as a rule postdischarge followed stimulus termination. Units displaying type II response could not follow high rates of stimulation, and showed habituation to repeated stimuli.

Taking these response types into consideration the 162 units studied were classified in two groups. Group A comprises 91 units which gave type I responses to visual stimuli. As a rule they showed type II responses to other sensory modalities. The re-



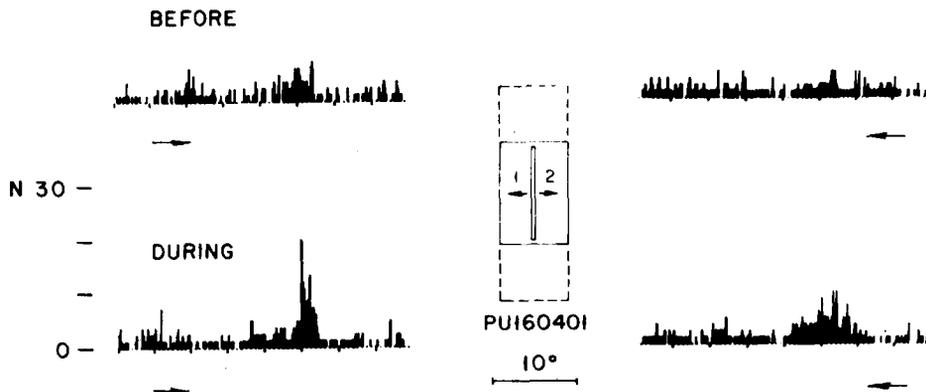


Fig. 2. Influence of the state of arousal in unit response to specific visual stimulation. The histograms illustrate the response of a Group A unit to a  $10^\circ \times 1^\circ$  slit displaced across its receptive field ( $v = 21.6^\circ/\text{sec}$ ) in the directions indicated by the arrows. Notice the improvement of the response during arousal promoted by simultaneous somatic and auditory stimulation. Data of each histogram gathered in 15 trials. The whole extent of the graph corresponds to  $40^\circ$  on the tangent screen. Ticks along abscissae represent  $5^\circ$  intervals. Insert illustrates receptive field organization: continuous line, excitatory region; dashed lines, inhibitory flanks.

maining 71 units, belonging to group B, displayed exclusively type II responses to one or more sensory modalities.

Under our experimental conditions, in the absence of intentional sensory stimulation units isolated in the pulvinar presented a rhythmic spontaneous activity characterized by the presence of cyclic bursts of spikes. EEG recorded from the parietooccipital region displayed the slow-wave pattern associated with drowsiness or with the initial stages of sleep. In the great majority of units isolated in the pulvinar generalized sensory stimulation promoted an alteration in the pattern of the spontaneous activity resulting in a suppression of the rhythmic burst activity (response type II). Under these conditions cortical slow-wave activity was substituted by the higher frequency pattern associated with arousal. An example of the modification of the pattern of spontaneous activity (or response type II) is presented in Fig. 1A. In this example it is shown that somatic as well as auditory stimulation produce an alteration in the interspike intervals, characterized by the suppression of short intervals. During the stimulation period the response of this unit became more regular and the short intervals characteristic of the 'bursty' activity disappeared. An analysis of the number of events per unit time shows

---

Fig. 1. Example of a type A unit. This unit, isolated in the dorsal portion of  $P_{VIIg}$ , shows a concentric receptive field localized in the vicinity of the vertical meridian in the lower contralateral visual quadrant (see inserts on the left). A: the alteration of the inter-spike intervals (ISI) during somatic (S) and auditory (A) stimulation. Arrows indicate stimulus onset and termination. Notice the disappearance of short intervals during sensory stimulation. B: histogram showing the response of the unit to a  $5^\circ$  luminous spot presented at the center of the receptive field. Notice the tonic OFF response. In C the spot was enlarged resulting in a marked inhibition of the OFF response. When the stimulus was circumscribed to the surrounding region a weak ON-response was observed (D). Stimulus duration indicated by the continuous line. Data for each histogram collected from 30 trials. The calibration in spikes/sec (sp/s) applies to B, C and D.

TABLE I

Pulvinar region	Group A	Group B	
		Multimodal	Unimodal
P $\alpha$ , P $\beta$ , P $\beta$	2	15	4
LPc	0	9	4
P $\mu$	24	5	1
P <sub>vlg</sub>	65	11	14

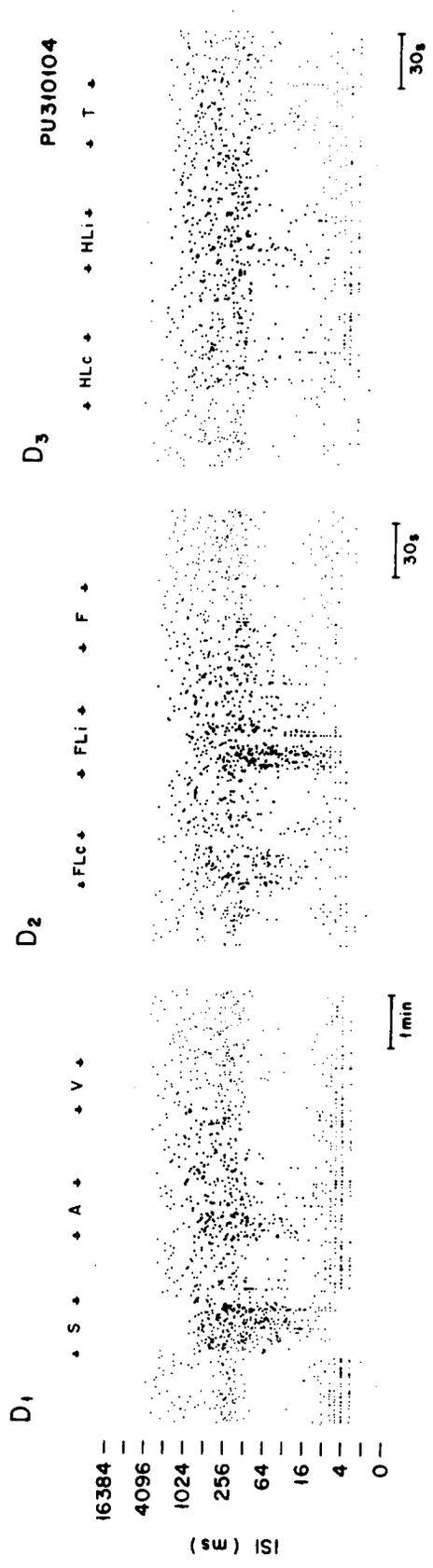
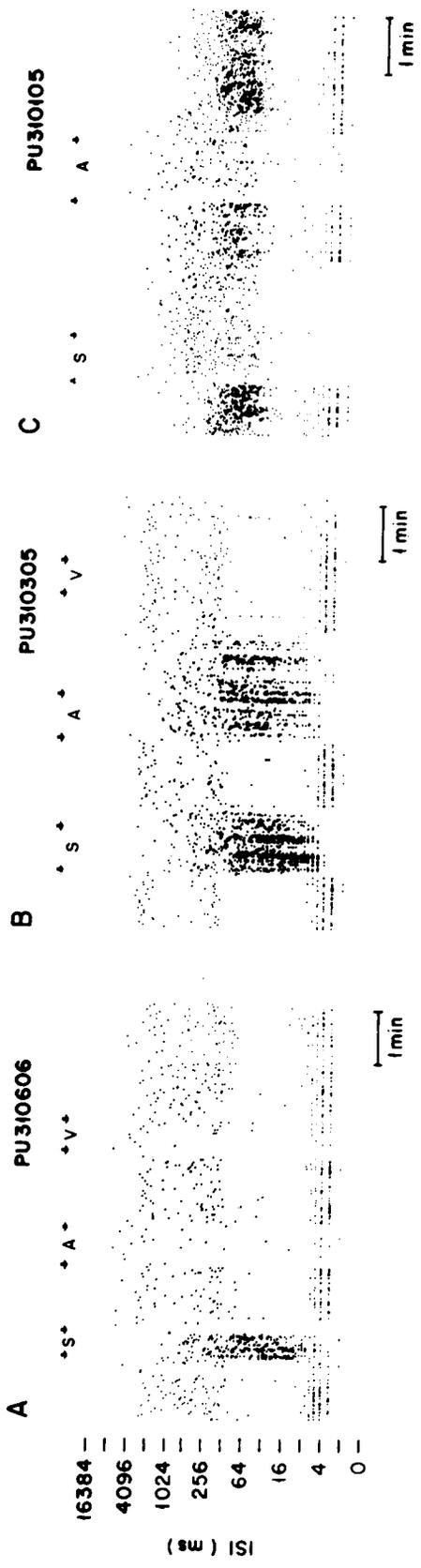
that during stimulation there is a reduction of the average frequency of firing of the unit, associated with the suppression of the rhythmic discharge pattern.

As a rule it was not possible to characterize the trigger features of adequate stimuli producing type II responses. For example, units with a type II response to somatic stimulation could be activated by stimuli applied over a large area of the contralateral body surface. Occasionally ipsilateral stimulation of the fore and hindlimb extremities were effective. Flickering or diffuse light were effective stimuli in promoting type II visual responses. We did not attempt a systematic study of the parameters of auditory stimuli, however complex natural sounds were more effective than sounds such as pure tones or 'clicks'.

#### Group A units

When isolated visual stimuli were applied while the unit was presenting a cyclic burst type of activity the evoked responses were irregular or totally absent. On the other hand, if isolated visual stimuli were applied after suppression of the bursty activity clear cut type I evoked responses were obtained. For this type of response it is possible to define a receptive field localized in the contralateral visual field<sup>13</sup>. The unit illustrated in Fig. 1 is an example of a group A unit showing a receptive field with concentric arrangement displaying center-periphery antagonism. This unit shows a tonic OFF-response to a light stimulus (5° spot) circumscribed to the center of the field (Fig. 1B). The center-surround antagonism is demonstrated by the reduction of the unit response to a larger spot, 20° in diameter (Fig. 1C), also centered in the receptive field. The temporal correlation between stimulus and response is evident (Fig. 1B, C and D).

Fig. 3. Examples of type B multimodal units presenting type II responses to stimuli of different sensory modalities. A: unit responding with excitatory desynchronization to somatic stimulation (S) and displaying inhibitory desynchronization to both auditory (A) and visual (V) stimuli. B: unit showing excitatory desynchronization to both somatic and auditory stimuli. Notice postdischarge following auditory stimulation and the absence of response to visual stimuli. C: example of inhibitory desynchronization of a unit responding to both somatic and auditory stimuli. D: the unit PU310104 shows response to somatic stimulation and only a slight alteration in the discharge pattern following auditory stimuli, being unresponsive to visual stimulation. During the period indicated by S in D<sub>1</sub> somatic stimulation was sequentially applied to various body regions. D<sub>2</sub> and D<sub>3</sub> illustrates the response of the same unit when somatic stimulation was applied to the contralateral and ipsilateral forelimbs (FL<sub>c</sub> and FL<sub>i</sub>), to the face (F), contralateral and ipsilateral hindlimbs (HL<sub>c</sub> and HL<sub>i</sub>) and to the trunk (T). Notice the various degrees of alterations in the spontaneous activity promoted by the stimulation of different body regions. Notice the faster time base in D<sub>2</sub> and D<sub>3</sub>.



Units responding to visual stimuli showed a variable degree of dependence on the state of arousal. An example of this dependency is presented in Fig. 2.

This figure illustrates the response of a directional unit with inhibitory flanks to a  $10^\circ \times 1^\circ$  slit displaced across its receptive field, under two conditions: upper histograms show the unit response to a bright bar moved across the screen in the direction indicated by the arrows while the animal displayed slow wave EEG; the lower histograms show the unit response to the same stimulus while the animal was displaying a desynchronized EEG. Arousal was promoted by the presentation of complex sound patterns through an earphone and by simultaneous tactile stimulation of the body surface. A clear improvement of the response was obtained when testing the unit during the suppression of its cyclic activity.

Type II responses were observed in all group A units tested (73 out of 91). A detailed analysis of the receptive field characteristics of visual units will be presented in a following paper<sup>13</sup>.

#### *Group B units*

Using somatic, auditory, visual and olfactory stimuli it was shown that 40 units (63.5%) presented type II responses to more than one sensory modality (B, multimodal units), while 23 units (36.5%) presented this type of response to a single sensory modality (B, unimodal units) (Table I). In 8 units belonging to this group, stimulus modality specificity was incompletely tested, therefore they could not be classified in either category.

*B, multimodal units.* Among the multimodal units ( $N = 40$ ) there was a great predominance of units that responded to both somatic and auditory stimuli. Cells activated by these sensory modalities represent 47.5% of the units included in this category. The second most frequent observed group (25%) is the one including units showing responses to somatic, auditory and visual stimuli. The remaining 27.5% correspond to units activated by other combinations of the various sensory modalities. Olfactory stimulation which was only tested in 18 of these units was effective in 55% of these cases.

The type of response most frequently evoked was the suppression of the rhythmic pattern of neuronal discharges, which could be accompanied or not by a marked alteration in the mean frequency of discharge. This pattern of alteration was found in 55% of the units showing type II responses. The remaining units presented a different type of response characterized by an increase (excitation) or a decrease (inhibition) of the mean frequency of discharge, but without appreciable alteration of the rhythmic pattern of discharge.

Suppression of burst activity associated with an increase in the mean frequency of discharge (excitatory suppression) was the type of response most frequently (34%) observed. An example of this type of alteration can be seen in Figs. 3A, B and 4A.

The same unit could display different patterns of activation in response to stimuli of different modalities as shown in Fig. 3A. Somatic stimulation promotes excitatory suppression while auditory and visual stimuli promote an inhibitory suppression. However a greater number of units (61.5%) display the same pattern of alteration of the activity in response to stimuli of different sensory modalities. The unit illustrated in

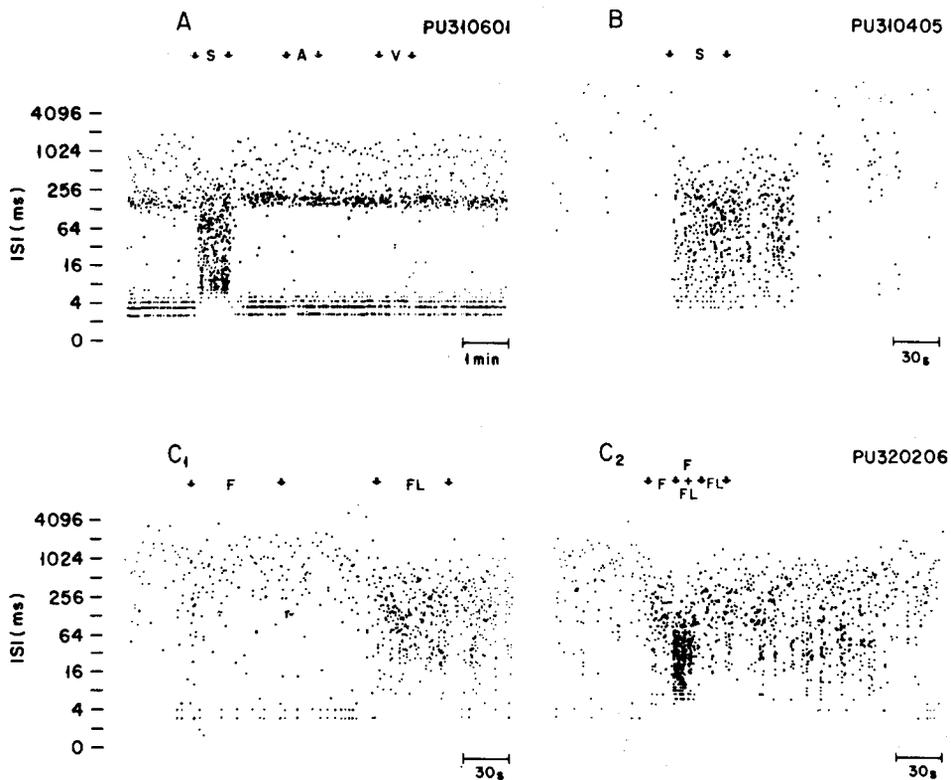


Fig. 4. Examples of type B unimodal units responding to somatic stimuli. A: unit showing strong excitatory desynchronization during somatic (S) stimulation, contrasting with the absence of response following auditory (A) and visual (V) stimulation. B: long lasting postdischarge following somatic stimulation. C: facilitatory effect. Unit PU320206 responds weakly ( $C_1$ ) to independent stimulation of face (F) and forelimb (FL). Simultaneous stimulation of both regions, F + FL in  $C_2$ , promotes a stronger response.

Fig. 3B responds with excitatory suppression to both somatic and auditory stimulation, while that illustrated in Fig. 3C shows inhibitory suppression to similar stimuli. Furthermore an unit could display different magnitude of responses depending on the region stimulated. Fig. 3D illustrates responses of an unit to somatic stimuli applied to different regions of the contralateral and ipsilateral body surface.

*B, unimodal units.* The most frequently found category of B, unimodal units corresponds to those activated by somatic stimuli. Of the 23 units included in this group 16 were selectively activated by somatic stimulation.

The response patterns of three units belonging to this group are illustrated in Fig. 4. Fig. 4A is an example of an unit showing excitatory suppression of the bursty activity promoted by somatic stimulation. Auditory and visual stimuli did not alter the 'bursty' type of spontaneous activity presented by this cell, which is characterized by the grouping of interspike intervals in two bands with the average about 4 and 128 msec. The response pattern presented by unimodal units showed, as rule, all the characteristics described for type II responses, including after-discharge (Fig. 4B) and habituation.

Facilitatory effects promoted by simultaneous stimulation of two regions of the receptive field is illustrated in Fig. 4C. This unit showed a negligible response to stimuli applied to the face and a weak response to contralateral forelimb stimulation (Fig. 4C<sub>1</sub>). Simultaneous stimulation of the face and forelimb promoted a strong excitatory suppression as shown in Fig. 4C<sub>2</sub>.

The remaining units included in this group were specifically activated by visual (4 units), auditory (2 units) and olfactory (1 unit) stimuli.

#### *Localization of units in pulvinar*

Reconstruction of the penetrations in which the 162 units studied in this paper were obtained indicate that these neurons belong to subnuclei  $P\alpha$ ,  $P\beta$ ,  $Pl$ ,  $LPc$ ,  $P\mu$  and to the ventrolateral group of the pulvinar ( $P_{vlg}$ ) which comprises subnuclei  $P\mu_1$ ,  $P\delta$ ,  $P\delta_1$ ,  $P\eta$  and  $P\gamma^{11}$ . These subnuclei correspond to Olszewski's pulvinar medialis, lateralis and inferior<sup>23</sup>.

The great majority of group A units (89/91) was recorded in  $P\mu$  (24) and  $P_{vlg}$  (65) (see Table I). The remaining two units belonging to this group were isolated in  $Pl$ , a subnucleus of the pulvinar lying in the mesial border of pulvinar medialis.

Group B units were found distributed throughout the pulvinar contrasting with group A units which were only isolated from  $P\mu$ ,  $P_{vlg}$  and  $Pl$  (see Table I). As in group A the highest percentage of B units was obtained in the subnuclei comprising  $P_{vlg}$  (25/71). Within  $P_{vlg}$  these units predominate in its dorsal portion, the region corresponding to subnucleus  $P\mu_1$ . The remaining units were distributed in  $LPc$  (13),  $P\beta$  (17),  $P\mu$  (6),  $P\alpha$  (1) and  $Pl$  (1).

## DISCUSSION

The A type units described in the present paper show characteristics similar to those described for visually driven units observed in the pulvinar of various species<sup>14,25,33</sup>. In addition we have shown that the response of pulvinar units to specific visual stimuli is dependent on the animal's state of arousal in a way similar to that reported for units in the inferotemporal cortex of the rhesus monkey<sup>15</sup>.

It is interesting to note that we found a high percentage of units driven by more than one sensory modality. This result is in contrast with the findings of Mathers and Rapisardi<sup>24</sup> who did not find multimodal units in their study of the pulvinar of the squirrel monkey. However, multimodal units, showing characteristics similar to those reported for type B units of the present paper have been described in regions homologous to the pulvinar, in non-primates<sup>7,17</sup>. The presence of multisensory responses in the pulvinar of the cat has been demonstrated by means of the evoked potential technique<sup>18,21</sup>. Conflicting results were obtained in single unit studies of this region. In two of these studies the presence of polysensory units in the pulvinar of the cat has been reported<sup>17</sup>, while Chalupa et al.<sup>7</sup> in their study of the posterior thalamic region of the cat reported that only 3 of the 167 units studied responded to more than one sensory modality.

Various studies, recently reviewed by Chalupa<sup>5</sup> give support to the participation of the pulvinar in the processing of visual information. Therefore most of the single unit

analysis of this region has been concerned with the study of the properties of visual receptive fields. Consequently the large number of 'unresponsive' units found in the pulvinar by other authors<sup>14,25,33</sup> may, in reality, correspond to units having properties similar to those described for type B units of the present paper. Units showing multisensory convergence frequently displayed similar types of responses following stimulation of different sensory modalities. Therefore the sensory interactions observed in the pulvinar are of a similar nature as those observed in the mesencephalic reticular formation, where the responses of a given cell to its different inputs were usually similar<sup>2</sup>. In the pulvinar we also have some units which display different responses to stimuli of different modalities.

The relative percentage of type A and type B units reported in this paper possibly does not reflect their actual distribution. Type A units were more frequently found in the lateral portion of this nucleus where a greater number of penetrations were carried out. A more valid relationship is obtained comparing their relative percentage in a given subnucleus. For instance it is interesting to note that no type A units were found in pars caudalis of the lateral posterior nucleus which is located in the lateral portion of the posterior thalamic region. In contrast a large percentage of type A units were found in subnuclei  $P_{\mu}$  and  $P_{vlg}$ , regions where two distinct topographic representations of the visual field have been reported<sup>12</sup>.

It is also worth noticing that a higher percentage of units showing multisensory convergence were observed in a region corresponding to the representation of the lower visual field in  $P_{vlg}$ . This preponderance may reflect the importance of multisensory integration in a region of the visual field more directly involved with the immediate surrounding.

The spontaneous activity observed in units recorded in the pulvinar of Cebus monkeys, under our experimental conditions, show a pattern of response similar to that described in other species (cat<sup>14,33</sup>, monkey<sup>25,30</sup> and man<sup>1</sup>). This type of activity may be related to slow wave sleep since the presence of bursts of activity in pulvinar neurons was shown to be related to the presence of slow cortical waves in the parieto-occipital region<sup>30</sup>. The fact that responses to specific visual stimuli in type A units were only observed during periods of desynchronization may suggest the participation of the pulvinar in the mechanisms of visual selective attention, a suggestion already brought forth by Chalupa<sup>5</sup>. This interpretation is supported by studies which show that lesions in the pulvinar result in alterations of the pattern of eye movements involved in foveation, during discrimination tasks<sup>8</sup>, and also in reduction of the capacity to discriminate between complex visual stimuli<sup>6</sup>. Furthermore this region of the pulvinar receives a major input from the superior colliculus where cells have been shown to give an enhanced response to significant stimuli<sup>34</sup>.

Based on the description of pulvinar cell types and their synaptic connections it is possible to attempt an anatomofunctional correlation. Thus the two types of neurons described by Hajdu et al.<sup>16</sup> could be correlated with the two types of units described in the present paper. Units of type A present response characteristics that could be attributed to visual afferents originating from cortical<sup>24,26,31</sup> and collicular<sup>28</sup> regions, supplemented by multimodal afferents originating from B type units. Type A may therefore

correspond to the principal cells described by Hajdu et al.<sup>16</sup>. On the other hand, units of type B with characteristics that may be attributed to afferents originating from various cortical areas<sup>24,26,31</sup>, since they show multimodal responses, may correspond to the interneurons described in the pulvinar<sup>16</sup>.

Various anatomical studies have demonstrated the presence of synaptic glomeruli in the pulvinar<sup>16,22,23</sup>. This synaptic arrangement would allow the interaction of a wide diversity of afferents at the level of the principal cells.

The hypothesis proposed in which the B type units with their multimodal characteristics correspond to the interneurons, and the visually driven A units correspond to the principal cells is valid for those regions of the pulvinar in which topographical organized projections of the visual field have been reported<sup>12</sup>.

#### ACKNOWLEDGEMENTS

This research was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (TC-9467 and TC-16872), Banco Nacional de Desenvolvimento Econômico (FUNTEC-241), Financiadora de Estudos e Projetos (FINEP-445) and Conselho de Ensino para Graduados da UFRJ (CEPG/UFRJ).

The authors are grateful to our colleague C. E. Rocha-Miranda and to V. H. Perry of Oxford University for their comments on the manuscript. We extend our thanks to Mr. R. F. Bernardes for his unfailing technical assistance and Ms. Maria Luiza da Silva for secretarial help.

#### REFERENCES

- 1 Albe-Fessard, D., Arfel, G. et Guiot, G., Activités électriques caractéristiques de quelques structures cérébrales chez l'homme, *Ann. Chir.*, 17 (1963) 1185-1214.
- 2 Bell, C., Sierra, G., Buendía, N. and Segundo, J. P., Sensory properties of neurons in the mesencephalic reticular formation, *J. Neurophysiol.*, 27 (1964) 961-987.
- 3 Buser, P., Borenstein, P. et Bruner, J., Étude des systèmes 'associatives' visuels et auditives chez le chat anesthésié au chloralose, *Electroenceph. clin. Neurophysiol.*, 11 (1959) 305-324.
- 4 Calma, I., The activity of the posterior group of thalamic nuclei in the cat, *J. Physiol. (Lond.)*, 180 (1965) 350-370.
- 5 Chalupa, L. M., A review of cat and monkey studies implicating the pulvinar in visual function, *Behav. Biol.*, 20 (1977) 149-167.
- 6 Chalupa, L. M., Coyle, R. S. and Lindsley, D. B., Effect of pulvinar lesions on visual pattern discrimination in monkeys, *J. Neurophysiol.*, 39 (1976) 354-369.
- 7 Chalupa, L. M., Macadar, A. W. and Lindsley, D. B., Responses of pulvinar and lateralis posterior units to visual and auditory input in the cat: Interactions with cortex, lateral geniculate and superior colliculus, *Electroenceph. clin. Neurophysiol.*, 36 (1974) 210.
- 8 Christensen, C. A., Pulvinar lesions in monkeys produce abnormal eye movements during visual discrimination training, *Ass. Res. Vis. Ophthalm.*, 1977, 135p.
- 9 Chung, S. H., Lettvin, J. Y. and Raymond, S. A., The CLOOGE: a simple device for interspike interval analysis, *J. Physiol. (Lond.)*, 239 (1974) 63P-66P.
- 10 Fokin, V. F., Veskov, R. and Lyubimov, N. H., Polysensory interaction in the posterior ventrolateral thalamic nucleus in cats, *Bull. exp. Biol. Med.*, 81 (1976) 643-645.
- 11 Gattass, R., *Complexo Posterior Talâmico do Cebus Apella: Estudos Anatômico e Eletrofisiológico*, Doctor Thesis, Instituto de Biofísica, 1976, 149pp.

- 12 Gattass, R., Oswaldo-Cruz, E. and Sousa, Aglai, P. B., Visuotopic organization of the Cebus pulvinar: a double representation of the contralateral hemifield, *Brain Research*, (1978) in press.
- 13 Gattass, R., Oswaldo-Cruz, E. and Sousa, Aglai, P. B., Visual receptive fields of single units in the pulvinar of Cebus monkey, *Brain Research*, (1978) in press.
- 14 Godfraind, J.-M., Meulders, M. and Veraart, C., Visual properties of neurons in pulvinar, nucleus lateralis posterior and nucleus suprageniculatus thalami in the cat. A qualitative investigation, *Brain Research*, 44 (1972) 503–526.
- 15 Gross, C. G., Rocha-Miranda, C. E. and Bender, D. B., Visual properties of neurons in inferotemporal cortex of the macaque, *J. Neurophysiol.*, 35 (1972) 96–111.
- 16 Hajdu, F., Somogyi, G. and Tömböl, T., Neuronal and synaptic arrangement in the lateralis posterior-pulvinar complex of the thalamus in the cat, *Brain Research*, 73 (1974) 89–104.
- 17 Hotta, T. and Terashima, S., Correlation between activity of the visual cortex and the somatovisual interaction in the lateral thalamus of cats, *Brain Research*, 2 (1966) 160–172.
- 18 Huang, C. C. and Lindsley, D. B., Polysensory responses and sensory interaction in pulvinar and related posterolateral thalamic nuclei in cat, *Electroenceph. clin. Neurophysiol.*, 34 (1973) 265–280.
- 19 Ionescu, D. A., Postprimary flash evoked responses in unanesthetized night and day-active monkeys, *Exp. Brain Res.*, 7 (1969) 275–298.
- 20 Koenig, J. Q. and Frazier, D. T., Light sensitive neurons in the pulvinar nucleus of the cat, *Proc. Soc. exp. Biol.*, 130 (1969) 399–403.
- 21 Kreindler, A., Crighel, E. and Marinichescu, C., Integrative activity of the thalamic pulvinar-lateralis posterior complex and interrelations with the neocortex, *Exp. Neurol.*, 22 (1968) 423–435.
- 22 Majorossy, K., Réthelyi, M. and Szentágothai, J., The large glomerular synapse of the pulvinar, *J. Hirnforsch.*, 7 (1965) 415–432.
- 23 Mathers, L. H., Ultrastructure of the pulvinar of the squirrel monkey, *J. comp. Neurol.*, 146 (1972a) 15–42.
- 24 Mathers, L. H., The synaptic organization of the cortical projection to the pulvinar of the squirrel monkey, *J. comp. Neurol.*, 146 (1972b) 43–60.
- 25 Mathers, L. H. and Rapisardi, S. C., Visual and somatosensory receptive fields of neurons in the squirrel monkey pulvinar, *Brain Research*, 64 (1973) 65–83.
- 26 Ogren M. and Hendrickson, A., Pathways between striate cortex and subcortical regions in *Macaca mulatta* and *Saimiri sciureus*: evidence for a reciprocal pulvinar connection, *Exp. Neurol.*, 53 (1976) 780–800.
- 27 Olszewski, J., *The Thalamus of the Macaca mulatta. An Atlas for use with the Stereotaxic Instrument*, Karger, Basel, 93pp. 1952.
- 28 Partlow, G. D., Colonnier, M. and Szabo, J., Thalamic projection of the superior colliculus in the rhesus monkey, *Macaca mulatta*. A light and electron microscopic study. *J. comp. Neurol.*, 171 (1977) 285–318.
- 29 Suzuki, H. and Kato, H., Neurons with visual properties in the posterior group of the thalamic nuclei, *Exp. Neurol.*, 23 (1969) 353–365.
- 30 Thieffry, M., Burnod, Y., Poussart, Y. and Calvet, J., Synchronous modifications in the cortical and pulvinar unit activity during slow wave sleep, *Exp. Neurol.*, 55 (1977) 327–339.
- 31 Trojanowski, J. Q. and Jacobson, S., The morphology and laminar distribution of corticopulvinar neurons in the Rhesus monkey, *Exp. Brain Res.*, 28 (1977) 51–62.
- 32 Whitlock, D. G. and Nauta, W. J. H., Subcortical projections from the temporal neocortex of *Macaca mulatta*, *J. comp. Neurol.*, 106 (1956) 183–212.
- 33 Wright, M. J., *The Visual Response Properties of Neurones in the Pulvinar and Lateral Posterior Nuclei of the Thalamus and the Lateral Supra-Sylvian Area of the Cortex of the Cat*, Ph.D. Thesis, University of Cambridge, 1971, 251pp.
- 34 Wurtz, R. H. and Mohler, C. W., Organization of monkey superior colliculus: enhanced visual response of superficial layer cells, *J. Neurophysiol.*, 39 (1976) 745–765.