

VISUAL RECEPTIVE FIELDS OF UNITS IN THE PULVINAR OF CEBUS MONKEY

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

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, RJ (Brazil)

(Accepted May 11th, 1978)

SUMMARY

Visually driven units, isolated in the ventrolateral group — P_{vlg} (109) and in subnucleus $P\mu$ (33) of the pulvinar of the cebus monkey, were studied in acute and chronic preparations under nitrous oxide N_2O/O_2 anesthesia during periods of EEG arousal. Taking into consideration the response properties to static or moving stimuli as well as the organization of the receptive fields, units isolated in the pulvinar were subdivided into 8 groups. Units displaying dynamic properties predominate over static ones. Static units were classified in 3 groups; of these, one showed uniform receptive fields; the remaining two groups, with non-uniform RFs, were further subdivided in terms of orientation selectivity. By testing for directional sensitivity, organization of the RFs and orientation selectivity, the dynamic units were divided in 5 groups. Among these there was a predominance of directional units, displaying uniform RFs and showing orientation selectivity. Although the receptive fields would extend into the ipsilateral hemifield (up to 10°), their centers were always located in the contralateral visual hemifield.

Binocularly driven units predominate in both static and dynamic categories.

INTRODUCTION

The participation of the pulvinar in the analysis of visual information has been suggested by anatomical^{9,24,39,41} and electrophysiological^{1,14,16,27} studies. Light-evoked slow potentials²² and single unit responses²⁷ have been reported in regions of the pulvinar which receive projection from the superficial layers of the superior colliculus^{3,25,32,38} and establish reciprocal connections with cortical areas involved in higher levels of visual information processing, namely striate^{4,5,7,30,39}, peristriate^{7,26,39} and inferior temporal cortex^{39,42}. In a previous study we reported a double represen-

tation of the contralateral visual hemifield in the pulvinar of the cebus monkey, coextensive with pulvinar ventrolateral group (P_{vlg}) and subnucleus $P\mu$ ¹⁴. P_{vlg} and $P\mu$ correspond, respectively, to pulvinar inferior and part of pulvinar lateralis and to the lateral aspect of pulvinar lateralis according to Olszewski's nomenclature. In this paper we report on the visual properties of single units within these regions, and compare them to those described for the superior colliculus^{15,17,40} and cerebral cortex^{11,19,21}.

MATERIAL AND METHODS

This study is based on units isolated in the pulvinar of 17 *Cebus apella* monkeys, in 12 acute and 5 chronic preparations. Nine of the acute preparations were initially anesthetized with sodium pentobarbital (30 mg/kg, i.p.), two with thionembutal (20 mg/kg, i.v.) and one with Fabantol (Bayer, 15 mg/kg, i.v.). The chronic preparations received in each recording session an initial anesthetic dose of ketamine hydrochloride (Ketalar, Parke-Davis, 20 mg/kg) and were sedated during the recording sessions with a tranquilizer (Valium, Roche, 5 mg/kg). All animals, after anesthetic induction, were kept under analgesia during the recording sessions by ventilation with a gaseous mixture of N_2O/O_2 in a 7:3 ratio.

At the start of each penetration the projections of the fovea and blind spots on a tangent screen placed 57 cm away from the nodal points of the eyes were determined by means of a reversible ophthalmoscope. By adjusting the background lights, diffuse illumination of the screen with a luminosity of 1.0 ftL was achieved. The trigger features of the unit under study were determined by means of luminous stimuli of various configurations, with a luminosity 1 log unit above that of the background. Stimuli were retroprojected onto the screen by means of a hand-held projector. Receptive fields (RF) which were plotted on the screen by this method correspond to the 'minimal receptive fields' of Barlow².

Quantitative data and a permanent record of the observations were obtained by means of a computer (PDP-12) controlled system.

In this study two computer programs were used. The first displays two histograms of the cumulative number of events that occurred following the onset (ON) and interruption (OFF) of the stimulus presentation. The second program, used to plot receptive fields, also generates two histograms, one for each direction of stimulus displacement across the screen.

At the end of the last experiments the animals were deeply anesthetized and perfused. The brains were processed for microscopical examination in order to determine the position of the recording sites. A more detailed account of these procedures has been published elsewhere¹⁴.

RESULTS

In a previous publication we have shown that visually driven units responding to patterned stimuli are found in the ventrolateral portion of the pulvinar. This region

includes a double representation of the contralateral visual hemifield. One of them, occupying a smaller area, is coextensive with subnucleus P_{μ} , while the main representation extends across several subnuclei which comprise the ventrolateral group of the pulvinar (P_{vlg}). In our previous study the response of units isolated in these regions to visual stimuli was shown to be highly dependent on the overall state of arousal, as judged by the EEG recordings¹⁵. Therefore, care was taken in the present study to ensure that the units responses to visual stimulation were studied during periods of arousal promoted by stimulation of other sensory modalities.

A total of 142 units, isolated in the ventrolateral group of the pulvinar — P_{vlg} (109) and in subnucleus P_{μ} (33), were studied. As the functional properties of units isolated in these two regions do not differ significantly, they will be considered as a single population in the present paper.

Receptive field area and location

A wide variation of receptive field (RF) areas was observed, fields as small as 0.8 deg.sq. and as large as 1592 deg.sq. being found. The median of the distribution of RF areas is 69 deg.sq. the first and third quartiles corresponding to 28 deg.sq. and 156 deg.sq., respectively.

An attempt to correlate the area of the RFs with the different groups of units described in this paper did not yield statistically significant results. The only consistent observation was that the smallest areas always belonged to units with concentric receptive fields; nevertheless, concentric units with large RFs were also identified. We also observed that RF areas did not vary as a function of eccentricity ($r = 0.15$).

Although part of the receptive fields may extend across the vertical meridian up to 10° into the ipsilateral hemifield, their centers were always located in the contralateral visual hemifield. A strong predominance of representation of the central portion of the visual field was observed: 75% of the RF centers were located within 30° from the fovea.

Ocular dominance

In order to evaluate ocular dominance, cells were divided into 5 classes. Class 3 included units that responded equally well to stimuli presented to either eye. Classes 1 and 5 comprise those units which responded exclusively to the contralateral or ipsilateral eye, respectively. Units responding to both eyes, showing however a dominance by the contralateral or ipsilateral eye were included in groups 2 and 4, respectively.

Eye dominance was tested in 95 of the units included in this paper. A predominance of binocularly driven units (class 3) was observed (44%). Units driven preferentially by the contralateral eye (classes 1 and 2) were more frequent (40%) than those driven by the ipsilateral eye (classes 4 and 5 — 16%).

Unit classification

In order to systematize our findings and to enable a coherent presentation of the results we have classified the units according to their functional properties. With the

classification adopted it is possible to assemble all units under 8 groups, as shown in Fig. 1. The first tier of this classification rests on the differences in the response patterns of the units to stationary or moving stimuli. Units were classified as static when they showed brisk responses to stationary stimuli presented to their receptive fields. When the same stimulus was swept across their fields similar or weaker responses were obtained. In contrast, dynamic units showed poor or no response to stationary stimuli, brisk responses being obtained for stimuli displaced across their fields. Twenty-two units could not be categorized as static or dynamic, and were designated 'unclassified' (UNC). These units contributed, however, to data concerning receptive field area and location as well as ocular dominance. As a rule the dynamic units demonstrate a preferred velocity of stimulus displacement. Dynamic units predominate (90/120) over static ones (30/120). When confronted with the onset of a luminous stimulus (ON) or with its suppression (OFF), static units gave either tonic responses (11/19) or, less frequently, phasic ones (8/19). In contrast, dynamic units, when presented with similar types of stimuli, always displayed phasic responses.

Static units

Static units can be further subdivided on the basis of the organization of their receptive fields. Uniform units showed the same response type throughout their RFs; in contrast, the response type of non-uniform units was seen to vary within their fields.

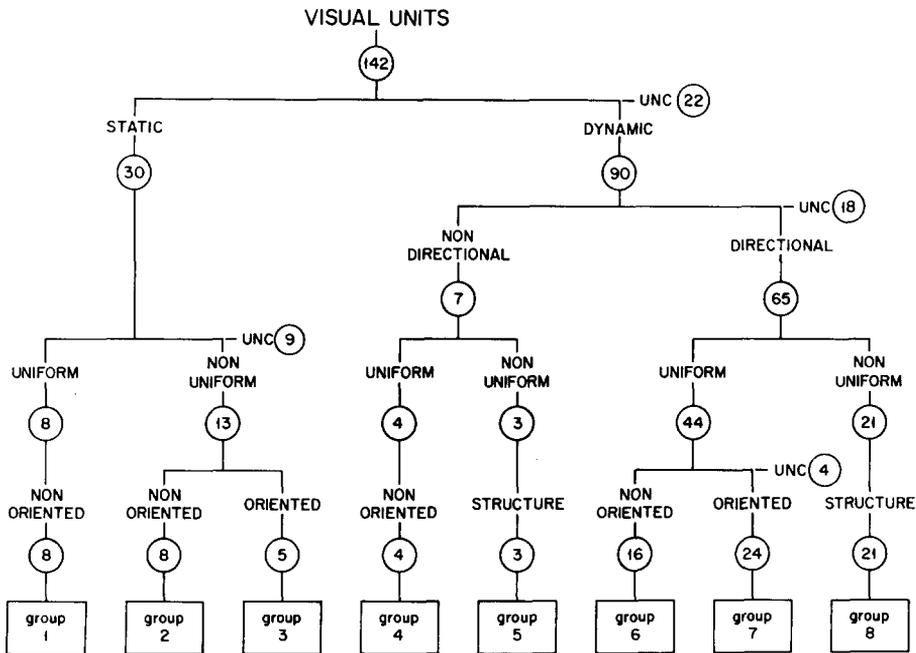


Fig. 1. Classification based on functional properties of neurons isolated in the pulvinar. When data available did not permit a reliable classification of a unit, this unit was included under a separate heading, unclassified, (UNC).

By testing for sensitivity to stimulus orientation, static units could be further subdivided. Five units, all showing non-uniform RFs, responded best to stimuli with a specific orientation. The remaining 16 units (8 uniform and 8 non-uniform) showed no preferential stimulus orientation. In terms of ocular dominance there was a predominance of binocularly driven units belonging to classes 2, 3 and 4 (12 out of 22), similarly, strictly contralateral dominance (class 1, 7 units) predominated over the ipsilateral one (class 5, 3 units).

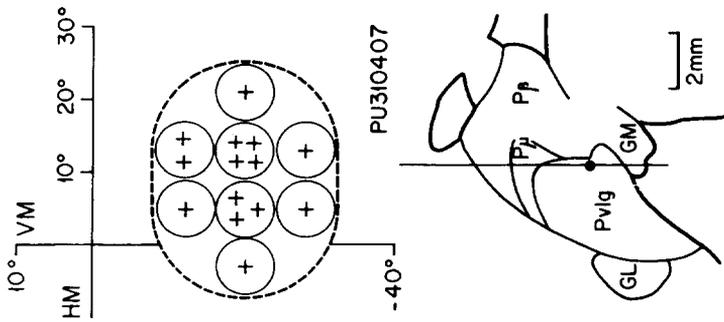
Uniform non-oriented (group 1). These units displayed the same response type to stimuli presented in any region of their receptive fields (ON = 3, OFF = 3 ON-OFF = 1), they also showed clear responses to diffuse light. The borders of their RFs are not clearly defined. One example of this type is illustrated in Fig. 2. This cell responds with a tonic ON discharge during the presentation of the stimulus (Fig. 2A, B and C). The response to a 7° spot varies in magnitude depending on the site of stimulus presentation within the RF, as indicated in the upper insert of Fig. 2.

Non-uniform non-oriented (group 2). Cells with non-uniform RFs were classified as group 2, provided that there was no sensitivity to stimulus orientation. These cells responded with either excitation or inhibition upon the presentation of ON or OFF stimuli in different regions of the receptive field. A discharge could always be evoked from the center of the RF either at the ON (5/7) or OFF (2/7) of the stimulus. These responses were of the tonic (3/7) or phasic (4/7) types. The response of the periphery was always phasic, whether the response of the center was phasic or tonic. An example of a unit showing these characteristics was illustrated in Fig. 1 of our previous paper¹⁵.

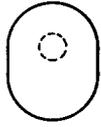
Non-uniform oriented (group 3). Units belonging to this group are distinguished from those described above by their preference for linear stimuli in a specific orientation within their receptive fields. The central portion of the field responded to static stimuli with a predominantly ON (4/5) or OFF (1/5) response which could be either tonic (4/5) or phasic (1/5). The surround was antagonistic with respect to the center. Different degrees of interaction between the responses of center and surround were observed. In the majority of instances tested, the response was of the phasic type. An example of a group 3 unit is illustrated in Fig. 3. An ON tonic response is obtained by the stimulation of the central portion of the field (Fig. 3B), while phasic, predominantly OFF responses are obtained from the flanks (Fig. 2C and D). The orientation selectivity of this unit is illustrated in recordings E – H of this figure.

Dynamic units

Dynamic units can be subdivided on the basis of the presence or absence of sensitivity to the direction of movement of the stimulus. The majority of dynamic units (65/72) showed a preferential direction of stimulus displacement. Non-directional dynamic units respond to a luminous spot displaced along any axis of the receptive field. Among dynamic units there was also a predominance (60 out of 73) of binocularly driven units (classes 2, 3 and 4), of these 36 units belonged to class 3. Strictly contralateral dominance (class 1) was observed in 11 units, while strictly ipsilateral dominance (class 5) was detected in only 2 units.



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50 -
0 -

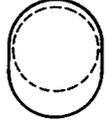


A

SPOT 7°



2s



B

SPOT 21° - RE



C

DIFFUSE LIGHT



D

SPOT 21° - LE



Non-directional

Uniform non-oriented (group 4). Of the 7 non-directional dynamic units, 4 displayed uniform RFs, showed phasic responses to stationary stimuli (ON-OFF), and gave brisk responses when the spot crossed the borders of the field. Clear responses were also obtained when the stimulus swept across the field at high velocities of displacement. In addition, good sustained responses could be elicited by 'jerky movements'.

Non-uniform with structure (group 5). Three of the dynamic non-directional units displayed non-uniform RFs. Two of them had a center-surround organization and one had regions of opposite response types. For units with a surround, such as the one illustrated in Fig. 4, the presentation of a static stimulus restricted to the central portion of the field produced a phasic response (Fig. 4B, upper). An annular stimulus sparing this portion of the field did not produce a response; however, the response obtained from the central portion was blocked by simultaneous stimulation of the surround (Fig. 4B, lower). The absence of directional selectivity is illustrated in Fig. 3C. The small difference in response amplitude observed for the vertical (1-6) and horizontal (3-4) directions of stimulus displacement may be attributed to the larger area of the RF activated when the slit was oriented parallel to the long axis of the RF.

Units with non-uniform RFs contrast with those having uniform RFs in two ways: they have smaller receptive fields and show a preference to low velocities of stimulus displacement.

Directional

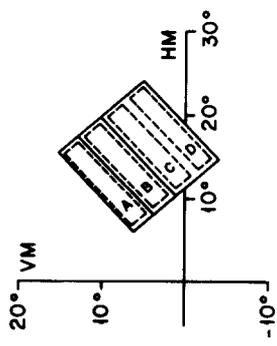
This is the most frequently found type of unit in the visually active region of the pulvinar. These units showed preference to slow velocities of stimulus displacement.

These units were further subdivided into two categories: the first includes units with uniform RFs (44/65) with or without orientation selectivity; the second includes units with non-uniform RFs, i.e. with structure (21/65).

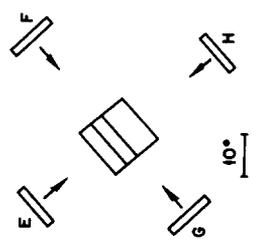
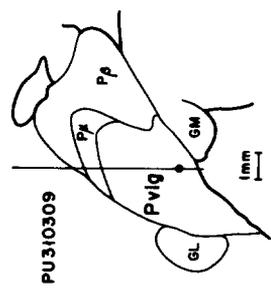
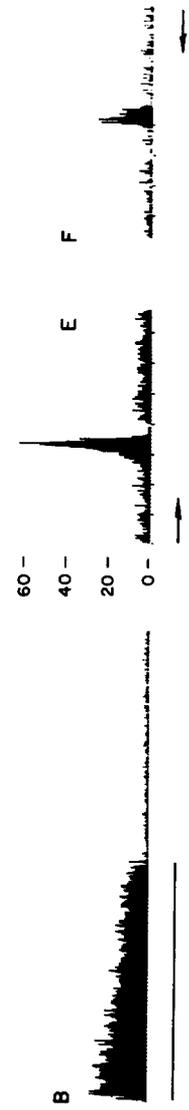
Uniform non-oriented (group 6). The units included in this group are characterized by the presence of uniform RF, and by the fact that they respond equally well to a luminous spot or to a slit displaced across their fields (Fig. 5A₅ and A₆). The majority

Fig. 2. Group 1 unit isolated in P_{VLG}. This unit gives a ON-tonic response to stimuli presented anywhere within its RF. In the upper insert the number of crosses indicates the relative magnitude of the response to a 7° spot. Note that the response magnitude does not vary appreciably when a 7° spot (A), a 21° spot (B) or diffuse light (C) are presented to the RF. Note the absence of response to stimuli presented to the left (LE) ipsilateral eye (D). Stimulus duration indicated by the continuous lines. A, B, C and D represent two ON-OFF poststimulus histograms of the cumulative number of events that occurred in each of 256 bins following the onset (ON) and interruption (OFF) of the stimulus presentation. The time span covered by each bin is adjustable. Each histogram represents the cumulative record of 30 trials. Abbreviations used in this and in other figures: VM, vertical meridian; HM, horizontal meridian; Sp/s, discharge rate in spikes per second; N, discharge rate in spikes per bin; GL, lateral geniculate nucleus; GM, medial geniculate nucleus; P_{VLG}, pulvinar ventrolateral group; P_μ, P_β, P_{γ1}, P_{γ2}, pulvinar subnuclei; Li, nucleus limitans; LE, left eye; RE, right eye.

Sp/° 20 -



N80 -



of units in this group is composed of unidirectional units (14/16), which show a great tolerance for stimulus deviation from the preferred orientation (broad tuning). The remaining two cells showed bidirectional responses, as shown in the RFPLOT histograms of Fig. 5B. In a few cases (3/16) inhibition was observed when the stimulus was displaced in a direction opposite to the preferred (null at 180°).

Uniform oriented (group 7). These cells are distinguished from the above by the presence of orientation sensitivity. They show weak responses to a spot displaced across their field. Tolerance to deviation from the preferred orientation was much smaller than in the previous group. This group is mainly composed of bidirectional cells (20/24); in some cells a null at 90° was observed. An example of a unit belonging to this group is illustrated in Fig. 6.

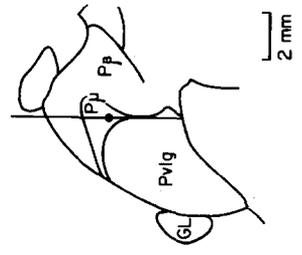
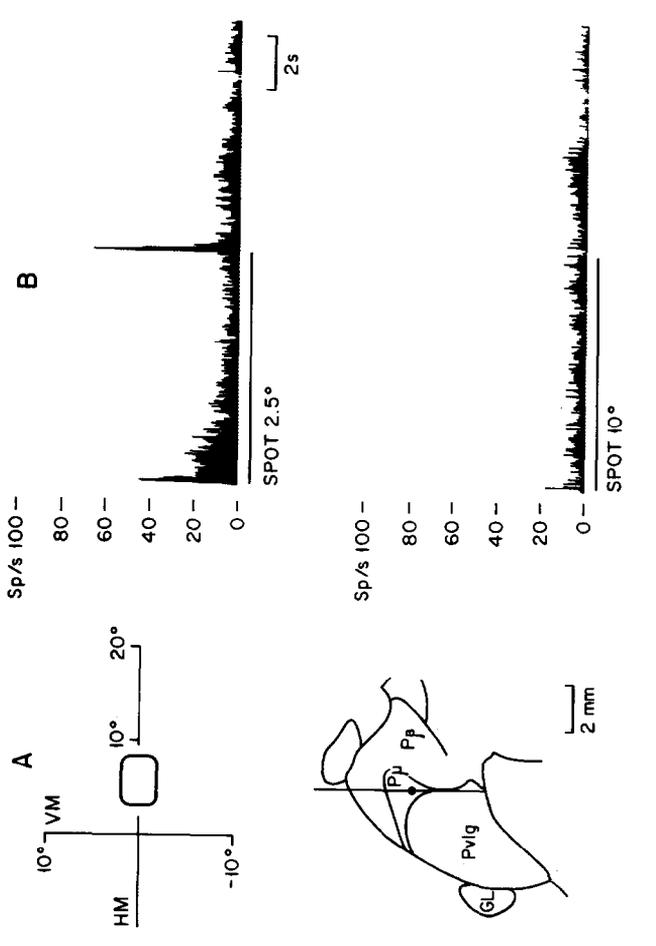
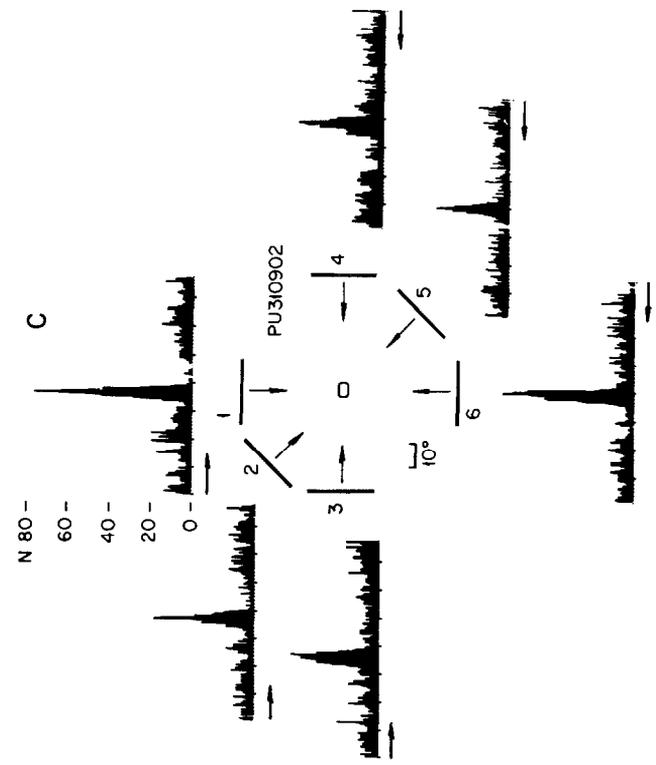
Non-uniform with structure (group 8). The units classified under this group are of two types. The first type includes cells (9/21) that show a RF with a single responsive area and inhibitory flanks. Most of these cells are unidirectional (8/9). Their responses to a long slit is less vigorous than when the length of the slit is adjusted to conform with the dimensions of the excitatory region of the receptive field. An example of one of these cells was presented as Fig. 2 of our previous paper¹⁵.

The second type included in this group comprises units that show receptive fields with more than one responsive area (12/21). At least one of the responsive areas show directional selectivity. These units show complex interactive responses when both centers are stimulated. Two units of this type are illustrated in Fig. 7. The RF of one of these units has two distinct unidirectional regions that are activated in sequence as the stimulus is swept across the field (Fig. 7, upper). The response of another unit also displaying two centers is illustrated in the lower part of Fig. 7. In the rectangular receptive field of this unit two regions were identified: the first, closer to the vertical meridian, gives an inhibitory response to both directions of stimulus displacement; the second, contiguous region, gives an excitatory response when the stimulus is displaced towards the periphery of the visual field and an inhibitory response for the opposite direction.

DISCUSSION

The units described in the present paper were isolated in the lateral region of the pulvinar within the boundaries of its ventrolateral group (P_{vlg}) and of subnucleus $P\mu$, regions where a double representation of the visual field has been described^{13,14}. This

Fig. 3. Response characteristics of a group 3 unit isolated in P_{vlg} . In A, B, C and D are illustrated ON-OFF histograms of the cell response to a stopped slit (2.5° wide) presented in the corresponding regions of the RF. Note the tonic ON-response in B contrasting with the phasic ON-OFF response of other regions. In E-H are illustrated histograms (RFPLOT) of the cumulative number of events that occurred in each of 256 bins for each direction of stimulus displacement across the screen. Histograms E-H correlate unit discharge with stimulus displacement in the directions indicated by the arrows. Note that the best response is obtained for the preferred stimulus orientation and that the cell does not show directional selectivity. Stimulus velocity = $13^\circ/\text{sec}$. Data gathered in 30 trials for each ON-OFF histogram and in 15 trials for each RFPLOT histogram.



region of the pulvinar corresponds to the inferior pulvinar and to the ventrolateral portion of pulvinar lateralis in Olzewski's classification³¹.

Receptive field area is of the same order of magnitude as reported in other species^{16,27,44}. The smallest receptive fields observed (0.8 deg.sq.) belonged to cells showing concentric receptive fields, a finding similar to that obtained by Wright⁴⁴ in the cat.

Although the two representations of the contralateral field in the pulvinar have different magnification factor functions¹⁴ in the present study we did not observe a significant difference in receptive field areas of units isolated in $P\mu$ and in P_{vlg} . The magnification factor in P_{vlg} was shown to vary as a function of eccentricity¹⁴; however, we did not find a correlation between RF areas and eccentricity.

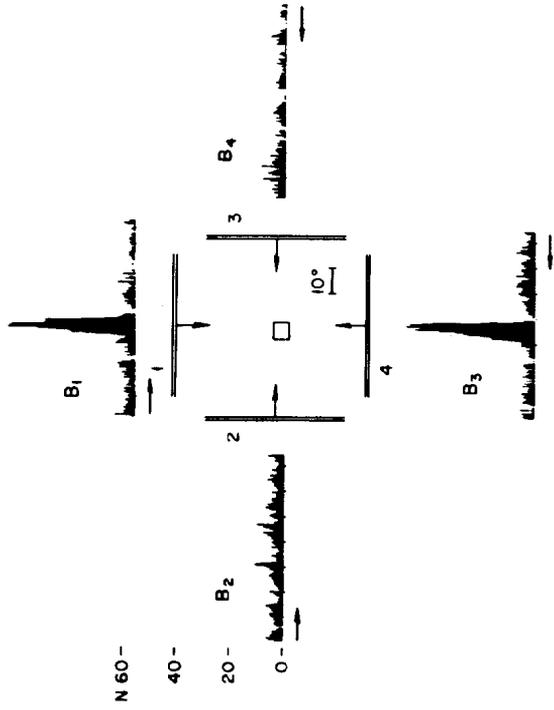
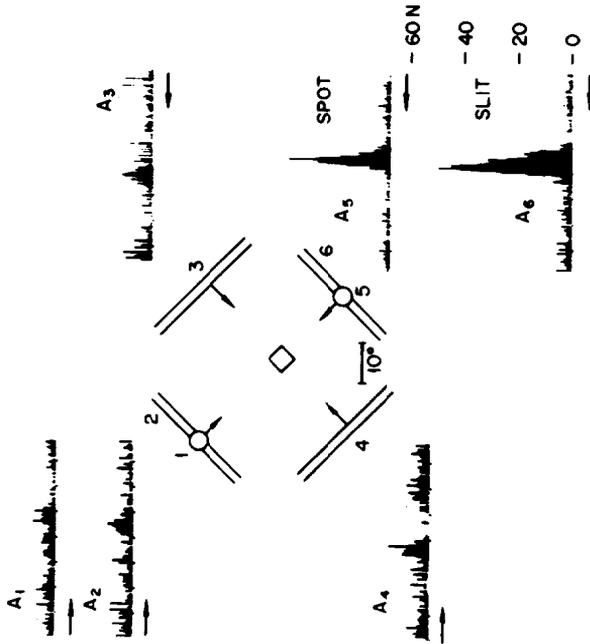
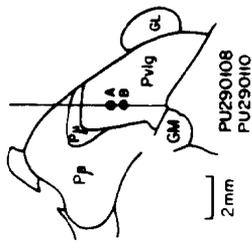
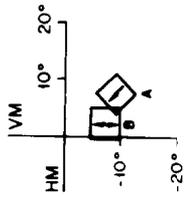
As described in the cat^{16,44} and squirrel monkey²⁷, the center of the RFs are always located in the contralateral visual hemifield. In contrast to inferotemporal cortex¹⁹, pulvinar receptive fields do not always include the region of the fovea.

In the pulvinar, as in other visual centers¹², static units responded with tonic or phasic discharges. The presence of tonic discharges as illustrated in Figs. 2 and 3 (and in Fig. 1 of a previous publication¹⁵) has not been reported in the pulvinar of other species^{16,27,36,37,44}. The majority of previous studies draw attention to the phasic characteristics and rapid habituation displayed by units isolated in the pulvinar.

Tonic and phasic discharges have been correlated with different types of ganglion cells (X, Y and W) that exhibit differential projections to the various layers of the dorsal lateral geniculate nucleus and to the superior colliculus²³. The presence of units exhibiting tonic and phasic discharges and, in addition, the identification of units showing orientation and direction selectivity suggests that pulvinar units possess properties which reflect those exhibited by its cortical and collicular afferents^{25,26,36,39}.

Although it is not easy to parallel our results with those reported in other primates under different experimental conditions²⁷, and with those described in the dorsal thalamus of the cat, in a region equivalent to pulvinar inferior and lateralis²⁹, some interesting comparisons may be attempted. In the squirrel monkey, Mathers and Rapisardi²⁷ reported that among static units the most frequently found types are those exhibiting diffuse and uniform receptive fields (34%), while in the dynamic group the movement sensitive cells predominate, representing 46.4% of the total population. These authors concluded that, as a rule, pulvinar cells do not have structure or surround. This is in disagreement with this report where non-uniformity and orientation sensitivity was present in the majority of the receptive fields. A similar predominance of directional selective units has been reported in the cat¹⁶.

Fig. 4. Example of a non-directional unit showing surround (group 5). This unit, isolated in $P\mu$, possesses a rectangular receptive field located at the level of the horizontal meridian near the fovea (A). B: *upper* — shows a phasic ON-OFF response evoked by a 2.5° diameter spot at the center of the RF; *lower* — shows the suppression of the response when the stimulus includes the surround (n = 30 trials). C: RFPLOT histogram of the response of the same unit obtained when a full slit (0.75° wide) is displaced across its RF, in the directions indicated by the arrows ($v = 9^\circ/\text{sec}$, n = 20 trials).



Static units showing concentric organization have been previously reported in the suprageniculate nucleus¹⁶ and in the pulvinar⁴⁴ of the cat. Concentric units with small RFs and responding exclusively to contralateral eye stimulation (3/8) display properties similar to those observed for units isolated in the dorsal lateral geniculate nucleus (GL)⁴³, a region which has been shown to project to the pulvinar³⁸. Units showing larger concentric RFs, as already shown by Wright⁴⁴, differ from units isolated in GL^{20,43} by displaying the same type of RF organization for both eyes (4/8) contrasting with the inhibitory input from one of the eyes observed in GL units. One unit displaying small concentric receptive field was driven by the ipsilateral eye.

Static oriented cells showing regions of opposing response type and mutual antagonism separated by linear boundaries, such as described by Hubel and Wiesel²¹ for cortical simple cells, were identified in cebus pulvinar and classed under group 3. Cells included in this group have an additional characteristic: stimuli applied to the central or principal region of its receptive field gave rise to tonic discharges, while those evoked from the flanks were of the phasic type. The presence of units showing some characteristics similar to cortical simple cells has also been reported in the pulvinar of the cat¹⁶. Cells displaying surround, such as those classed in groups 5 and 9 of the present work, have been described by Wright⁴⁴ in the pulvinar of the cat.

The only type of unit reported in this paper that has not been previously described by other authors in the pulvinar are some of those included in group 8, i.e., those units with dynamic properties, non-uniform receptive fields showing directional sensitivity, and displaying two distinct responsive areas within its field. In all units of this type the presence of two independent active areas within the RF was carefully investigated, and controls performed to assure that the doubling did not result from uncontrolled eye movements occurring during the study of the units.

The comparison of the types of units found in the pulvinar with those described in the various relay stations of the visual system leads us to an interesting question. What is the functional significance of units in the pulvinar showing properties similar to those described at different levels of the visual pathway? If we consider the pulvinar as a link between the geniculostriate and retinotectal systems²⁸ or even as a 'clearing house' as proposed for the visual cortex by Gouras¹⁸, the presence of RFs showing various degrees of complexity is in accordance with an associative or integrative function, and therefore enables this structure to participate in circuits involved in perceptual selection, as already suggested in a previous publication¹⁵. This role would also help to explain the preservation of form discrimination in both cats and monkeys after removal of striate and peristriate cortices³³⁻³⁵.

The presence of complex RFs and the dependence of visual responses on the

Fig. 5. Units A and B are directional uniform non-oriented (group 6), isolated in P_{v1g} in the course of a single penetration. RFPLOTS A₁-A₆ demonstrate the clear unidirectional response of unit A to both a 4.5° spot and a 2.5°-wide, full slit displaced across the RF. Each histogram was obtained from data gathered in 25 trials ($v = 22^\circ/\text{sec}$). RFPLOTS B₁-B₄ illustrate the bidirectional response of unit B to a 1° wide full slit. ($v = 7^\circ/\text{sec}$, $n = 20$ trials). Similar results were obtained when the slit was substituted by a spot.

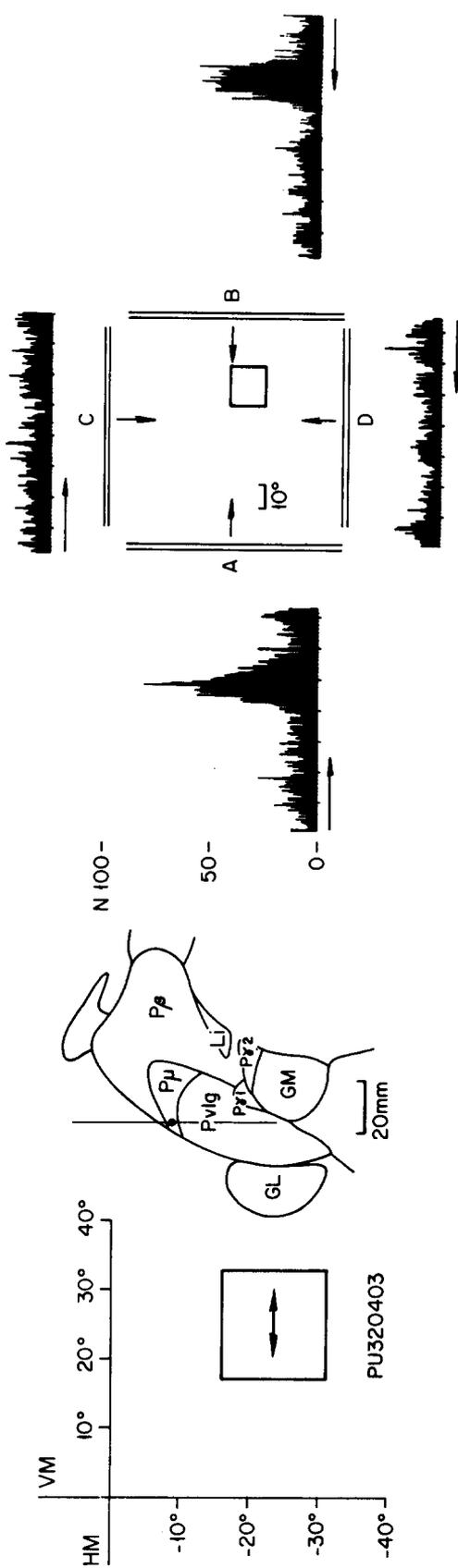


Fig. 6. Unit isolated in subnucleus P μ classified in group 7. This unit, with a RF located in the lower contralateral hemifield (inset) shows bidirectional response to a full slit 2.5° wide displaced across its field at a velocity of 4°/sec. Each RF PLOT histogram was obtained from 15 trials. Arrows indicate direction of stimulus displacement.

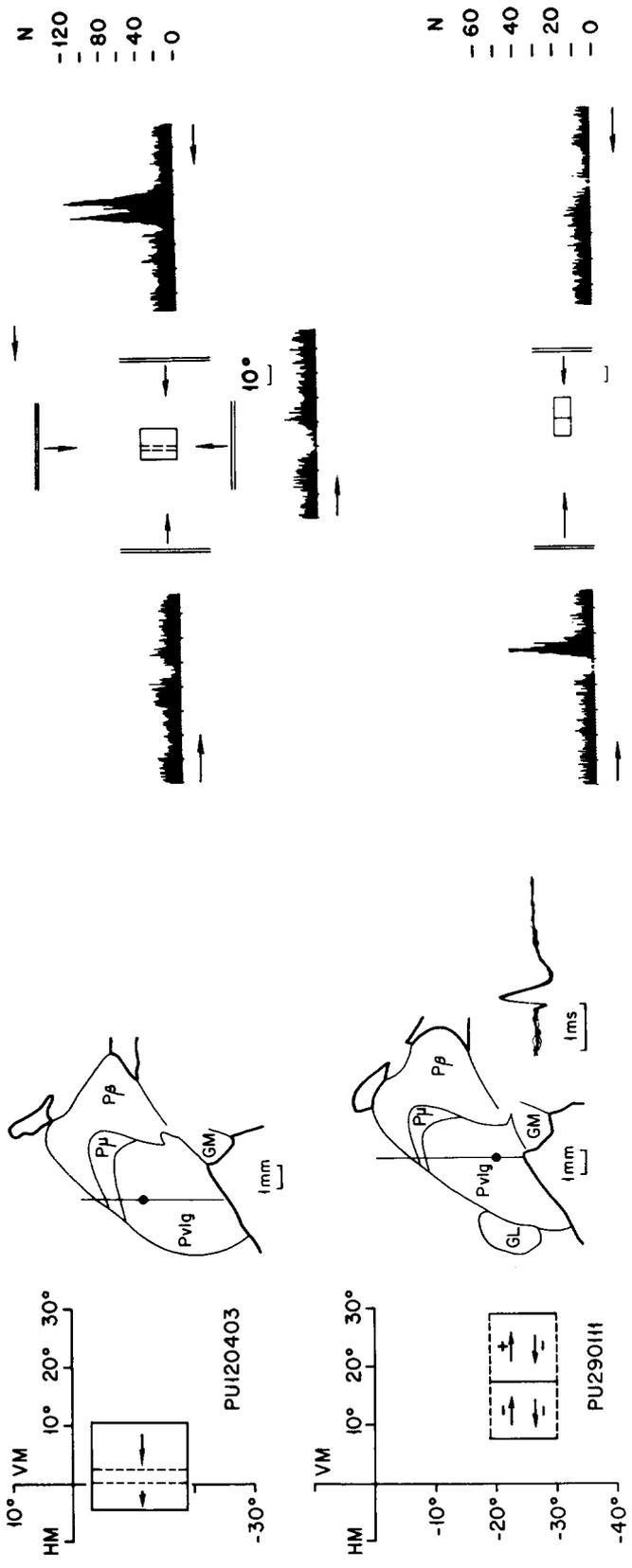


Fig. 7. Units showing complex receptive fields (group 8), isolated in P_{vis}. *Upper* — RFPLOT histograms (n = 50 trials) of the response of a unit displaying two independent unidirectional excitatory regions. The stimulus is a 1.5° wide full slit displaced at a velocity of 13°/sec. *Lower* — RFPLOT histograms (n = 20 trials) of the response of a unit displaying a bidirectional inhibitory response in one center, while the other center gave an excitatory response to the stimulus displaced in one direction and an inhibitory response to the opposite direction of stimulus displacement. Stimulus: a 2° wide full slit displaced at a velocity of 9°/sec.

state of EEG arousal observed in units isolated in the pulvinar could help to explain the severe deficit produced in animals by inferior pulvinar lesions, on discrimination tasks that require a high degree of visual attention⁸.

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. We also want to acknowledge the collaboration of Mr. W. Hoffmannbeck of Solótica Indústria e Comércio Ltda. in calculating and manufacturing the contact lenses used in the present study.

REFERENCES

- 1 Allman, J. M., Kaas, J. H., Lane, R. H. and Miezin, F. M., A representation of the visual field in the inferior nucleus of the pulvinar in the owl monkey, *Brain Research*, 40 (1972) 291-302.
- 2 Barlow, H. B., Blakemore, C. and Pettigrew, J. D., The neural mechanism of binocular depth discrimination, *J. Physiol. (Lond.)*, 193 (1967) 327-342.
- 3 Benevento, L. A. and Fallon, J. H., The ascending projections of the superior colliculus in the rhesus monkey (*Macaca mulatta*), *J. comp. Neurol.*, 160 (1975) 339-362.
- 4 Benevento, L. A. and Rezak, M., Extrageniculate projections to layers VI and I of striate cortex (area 17) in rhesus monkey (*Macaca mulatta*), *Brain Research*, 96 (1975) 51-55.
- 5 Benevento, L. A. and Rezak, M., The cortical projections to layers VI and I of striate cortex (area 17) in the rhesus monkey (*Macaca mulatta*): an autoradiographic study, *Brain Research*, 108 (1976) 1-24.
- 6 Burton, H. and Jones, E. G., The posterior thalamic region and its cortical projection in new world and old world monkeys, *J. comp. Neurol.*, 168 (1976) 249-302.
- 7 Campos-Ortega, J. A. and Hayhow, W. R., On the organization of the visual cortical projection to the pulvinar in *Macaca mulatta*, *Brain Behav. Evol.*, 6 (1972) 394-423.
- 8 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.
- 9 Chow, K. L., A retrograde cell degeneration study of the cortical projection field of the pulvinar in the monkey, *J. comp. Neurol.*, 93 (1950) 313-340.
- 10 Cynander, M. and Berman, N., Receptive-field organization of monkey superior colliculus, *J. Neurophysiol.*, 35 (1972) 187-201.
- 11 Dubner, R. and Zeki, S. M., Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey, *Brain Research*, 35 (1971) 528-532.
- 12 Fukada, Y. and Saito, H., Phasic and tonic cells on the cat's lateral geniculate nucleus, *Tohoku J. exp. Med.*, 106 (1972) 209.
- 13 Gattass, R., *Complexo Posterior Talâmico do Cebus apella: Estudos Anatômico e Eletrofisiológico*, Doctor Sci. Thesis, Instituto de Biofísica, UFRJ, 1976, 149 pp.
- 14 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*, in press.
- 15 Gattass, R., Sousa, Aglai, P. B. and Oswaldo-Cruz, E., Single unit response types in the pulvinar of the cebus monkey to multisensory stimulation, *Brain Research*, (1978) in press.
- 16 Godfraind, J.-M., Meulders, M. and Veraart, C., Visual properties of neurons in pulvinar, nucleus lateralis posterior and suprageniculatus thalami in the cat. I. Qualitative investigation, *Brain Research*, 44 (1972) 503-526.

- 17 Goldberg, M. E. and Wurtz, R. H., Activity of superior colliculus in behaving monkey. I. Visual receptive fields of single neurons, *J. Neurophysiol.*, 35 (1972) 542–559.
- 18 Gouras, P., The remapping of visual space, *Invest. Ophthalmol.*, 14 (1975) 719–723.
- 19 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.
- 20 Hubel, D. H. and Wiesel, T. N., Integrative action in the cat's lateral geniculate body, *J. Physiol. (Lond.)*, 155 (1961) 385–398.
- 21 Hubel, D. H. and Wiesel, T. N., Receptive fields and functional architecture of the monkey striate cortex, *J. Physiol. (Lond.)*, 195 (1968) 215–243.
- 22 Ionescu, D. A., Post-primary flash-evoked responses in unanaesthetized night- and day-active monkeys, *Exp. Brain Res.*, 7 (1969) 275–298.
- 23 Kelly, J. P. and Gilbert, C. D., The projections of different morphological types of ganglion cells in the cat retina, *J. comp. Neurol.*, 163 (1975) 65–80.
- 24 Le Gros Clark, W. E. and Northfield, D. C. W., The cortical projection of the pulvinar in the macaque monkey, *Brain*, 58 (1937) 470–477.
- 25 Mathers, L. H., Tectal projection to the posterior thalamus of the squirrel monkey, *Brain Research*, 35 (1971) 295–298.
- 26 Mathers, L. H., The synaptic organization of the cortical projection to the pulvinar of the squirrel monkey, *J. comp. Neurol.*, 146 (1972) 43–60.
- 27 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.
- 28 Mishkin, M., Cortical visual areas and their interactions. In A. G. Karczmar and J. C. Eccles (Eds.), *Brain and Human Behavior*, Springer-Verlag, New York, 1972, pp. 187–208.
- 29 Niimi, K. and Kuwahara, E., The dorsal thalamus of the cat and comparison with monkey and man, *J. Hirnforsch.*, 14 (1973) 303–325.
- 30 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.
- 31 Olszewski, J., *The Thalamus of the Macaca mulatta. An Atlas for Use with the Stereotaxic Instrument*, S. Karger, Basel, 1952, 93 pp.
- 32 Partlow, G. D., Colonnier, M. and Szabo, J., Thalamic projections of the superior colliculus in the rhesus monkey, *Macaca mulatta*, A light and electron microscopic study, *J. comp. Neurol.*, 171 (1977) 285–318.
- 33 Pasik, I. and Pasik, P., The visual world of monkeys deprived of striate cortex: effective stimulus parameters and the importance of the accessory optic system, *Vision Res.*, 11, Suppl. 3, (1971) 419–435.
- 34 Schilder, P., Pasik, P. and Pasik, T., Extrageniculostriate vision in the monkey. III. Circle vs. triangle and 'Red vs. green' discrimination, *Exp. Brain Res.*, 14 (1972) 436–448.
- 35 Sprague, J. M., Levy, J., Di Berardino, A. and Berlucchi, G., Visual cortical areas mediating form discrimination in the cat, *J. comp. Neurol.*, 172 (1977) 441–448.
- 36 Stewart, D. L., Towns, L. C. and Birt, D., Visual receptive-field characteristics of posterior thalamic and pretectal neurons in the rabbit, *Brain Research*, 57 (1973) 43–57.
- 37 Suzuki, H. and Kato, H., Neurons with visual properties in the posterior group of the thalamic nuclei, *Exp. Neurol.*, 23 (1969) 353–365.
- 38 Trojanowski, J. Q. and Jacobson, S., Peroxidase labeled subcortical afferents to pulvinar in rhesus monkey, *Brain Research*, 97 (1975) 144–150.
- 39 Trojanowski, J. Q. and Jacobson, S., The morphological and laminar distribution of corticopulvinar neurons in the rhesus monkey, *Exp. Brain Res.*, 28 (1977) 51–62.
- 40 Updyke, B. V., Characteristics of unit responses in superior colliculus of the Cebus monkey, *J. Neurophysiol.*, 37 (1974) 896–909.
- 41 Walker, A. E., *The Primate Thalamus*, University of Chicago Press, Chicago, Ill., 1938, 321 pp.
- 42 Whitlock, D. G. and Nauta, W. J. H., Subcortical projections from the temporal neocortex in *Macaca mulatta*, *J. comp. Neurol.*, 106 (1956) 183–212.
- 43 Wiesel, T. N. and Hubel, D. H., Spatial and chromatic interactions in the lateral geniculate body of the Rhesus monkey, *J. Neurophysiol.*, 29 (1965) 1115–1156.
- 44 Wright, M., *The Visual Response Properties of Neurons in the Pulvinar and Lateral Posterior Nuclei of the Thalamus and the Lateral Suprasylvian Area of the Cortex of the Cat*, Ph.D. Dissertation, University of Cambridge, 1973, 251 pp.