

## USE OF GABOR ELEMENTARY FUNCTIONS TO PROBE RECEPTIVE FIELD SUBSTRUCTURE OF POSTERIOR INFEROTEMPORAL NEURONS IN THE OWL MONKEY

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**Abstract**—The large receptive fields of inferotemporal neurons in the owl monkey were studied with visual stimuli whose luminance profiles were one-dimensional Gabor functions, i.e. sinusoidal gratings within Gaussian envelopes. The members of one set of such patterns all had a full bandwidth at half-amplitude of 0.8 octaves, but different center frequencies and spatial extents. These spatially restricted stimuli were ideal for determining whether one or more than one spatial frequency band projected onto discrete subsections of the neuron's receptive field. The other set of Gabor stimuli comprised sine waves within Gaussian envelopes of constant size, but with different center frequencies and hence different bandwidths. These stimuli allowed assessment of the neuron's spatial frequency selectivity across the full breadth of its receptive field. Results suggest that only one orientation band and one spatial frequency band provide an input onto each inferotemporal neuron under our experimental conditions. The preferred spatial frequencies found (0.2–0.6 c/deg) were all in the very low spatial frequency range for this animal. Calculations show that about 3.5–7.0 full cycles of the optimal grating usually cover the full width of the receptive field, but the observed spatial frequency tuning is not nearly as sharp as that which would be predicted according to phase coherent linear summation. Moreover, at the preferred spatial frequency, the peak response to gratings in the constant aperture series was generally less than the response to the same preferred spatial frequency in the constant relative bandwidth series. These results suggest either incomplete phase coherent summation from contributing subgroups, non-linear processing, or both.

Gabor functions    Receptive field substructure    Electrophysiologic studies    Inferotemporal  
neurons    Owl monkey    *Aotus trivirgatus*

### INTRODUCTION

The inferotemporal cortex subserves many functions essential for the identification of spatial patterns in the primate (for review see Gross, 1973). Receptive fields of inferotemporal neurons in the macaque monkey are large (frequently 10–20 deg across or even wider), usually include the fovea and often extend at least several degrees into the ipsilateral field (Gross *et al.*, 1972).

The owl monkey (*Aotus Trivirgatus*) studied here is an afoveal nocturnal primate whose spatial frequency sensitivity curve peaks at 1.5–2.0 c/deg with maximal resolution of about 10 c/deg (Jacobs, 1977). Its inferotemporal cortex receives a major input from the dorsolateral cortex (DL) which receives its predominant input from the second visual cortical area (VII) which derives its cortical projections from the

striate cortex (VI) (for review, see Weller and Kass, 1981).

As yet no analysis of the substructure of receptive fields of inferotemporal neurons in any primate has been attempted. We have attempted such an analysis by using the elementary signals of Gabor (1946) as test stimuli. This family of functions, some members of which resemble the receptive field profiles of simple cells in the striate cortex, are maximally localized simultaneously in space and spatial frequency (Marčelja, 1980). Such functions as stimuli are useful probes for any spatial filter for which the best evaluation of the substructure in space, spatial frequency and orientation would be of interest (see also Graham *et al.*, 1978).

### METHODS

#### *Preparation and recording*

A week before the first experiment with each animal, we injected ketamine (25 mg/kg) intramuscularly and infiltrated the scalp with a local anesthetic. We then opened the scalp and fixed two Kopf cylinders to the bone with screws and dental acrylic. Thereafter, the animal's head could be painlessly supported by rods attached to the plastic

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cylinders. On experimental days an intravenous cannula was inserted into a leg vein, and Brevital (methohexital sodium) 1 mg/cc was slowly injected until the animal fell asleep (a dose of 3 mg/kg was usually required). We then intravenously injected Flaxedil (gallamine trithiodide) (2 mg/kg) and intubated the animal. The animal was subsequently maintained on 70% nitrous oxide and 30% oxygen for light anesthesia and analgesia and respired with a Harvard pump adjusted to keep the  $p\text{CO}_2$  at 4.5–5.0%. Pavulon (pancuronium bromide) 0.1 mg/kg/hr was infused to eliminate detectable eye movements.

The scalp was infiltrated with a long-acting local anesthetic and then opened to permit exposure of the bone over the striate and inferotemporal cortex. A trephine hole was then made over the inferotemporal cortex and a 1 mm hole was drilled through the bone over the striate cortex. A local anesthetic, Ophthaine (propacane hydrochloride) 0.5%, was applied to each eye. Cycloplegia and mydriasis were produced with Cyclogel (cyclopentolate hydrochloride) 1%. Contact lenses were applied so as to focus each eye on a screen 57 cm away. Artificial pupils of 3.0 mm dia were used. The positions of the optic discs were back projected onto the screen. The inter-disc line was taken as the horizontal meridian (Allman and Kaas, 1971) and a line which perpendicularly bisected this line was taken as the vertical meridian.

Tungsten microelectrodes insulated with Parylene (Bak Electronics) were used. An electrode was first inserted through the small hole into the striate cortex. We advanced the microelectrode until a cell responding to both eyes was found. We then mapped the receptive field carefully for each eye alone. Then, using Risely biprisms, we adjusted visual fixation so that the two receptive fields were superimposed upon the screen. We then advanced an electrode through the thin dura into the inferotemporal cortex as normal to the surface as was technically possible. Some cells in IT were driven well by either eye, in which case stimuli were presented to only one eye. In other cases, binocular stimulation was required to enhance the response. Receptive fields were mapped using stationary and drifting slits of light or dark bars.

#### *Gabor stimuli*

Our main family of stimuli consisted of sinusoidal or cosinusoidal gratings whose contrast was spatially attenuated by Gaussian envelopes of different widths (Fig. 1). Transparencies of these patterns were produced by photographing the relevant displays as generated on a 608 Tektronix oscilloscope using an image generator (Innisfree, Inc.). All scope patterns were photographed without changes in contrast settings or mean luminance. Contrast was set for the mid-range of the gamma curve of the film used.

Two classes of Gabor stimuli were used. In the "constant relative bandwidth" series, the full bandwidth of all gratings was 0.8 octave at half-amplitude regardless of the grating's nominal spatial frequency.

These stimuli, limited in spatial extent (Fig. 1A–C), were drifted across the receptive field to stimulate its successive subsections. Transparencies of odd-symmetric and "on-center" even-symmetric functions were made using nominal spatial frequencies which covered a seven octave range from 0.05 to 6.4 c/deg in one-half octave steps.

In preliminary studies on the cat striate cortex we tested both odd-symmetric and even-symmetric stimuli on several complex cells. Simple cells should show a phase dependence related to the position of the particular Gabor stimulus used, but at the complex cell stage response patterns were essentially the same whether odd-symmetric or even-symmetric stimuli were used. In the inferotemporal cortex all cells found were of the complex cell type. Thus, as a matter of experimental convenience, we used only the "on-center" even-symmetric stimuli to study inferotemporal neurons.

In the second class of Gabor stimuli, the "constant aperture" series, the full width of the Gaussian envelope at half-maximal contrast always subtended 25°. These stimuli were used to stimulate an entire receptive field. The spatial frequencies were spaced in one-quarter octave steps covering the same range as the constant bandwidth series. Peak contrasts for the constant relative bandwidth and constant aperture series were closely matched at 30%. Mean luminance of the screen at our usual projection distance was 35 cd/m<sup>2</sup>. At a mean luminance of 11.4 cd/m<sup>2</sup>, spatial frequencies up to 8 c/deg can be detected by the owl monkey at this contrast (Jacobs, 1977).

Gabor functions were drifted across the receptive field at constant velocities low enough so that the individual bars of a grating were distinguishable to the experimenters with minimal reduction of apparent contrast when drifting stimuli in the high spatial frequency range were observed. Temporal frequencies at which preferred spatial frequencies were tested ranged from 2 to 10 Hz.

The stimuli were presented at a constant velocity so that all parts of the receptive field could be sequentially stimulated while the duration of stimulation at any given position was kept brief within each trial so as to minimize habituation. In this type of experiment the effect of temporal factors on the observed spatial frequency bandwidth cannot be directly assessed. In theory, a better way of studying differences between receptive field center and periphery might have been to present grating patches of varying spatial frequencies at constant temporal frequency at several fixed positions. However, these cells habituated so rapidly to any spatially fixed stimulus that this approach was impractical here.

Stimuli were presented with pauses of several seconds between successive presentations. Longer rest intervals made little difference. At least 20 sweeps were taken to construct each average response histogram. The histogram consisted of 100 bins with the width of each bin generally set at 50 msec. In carrying

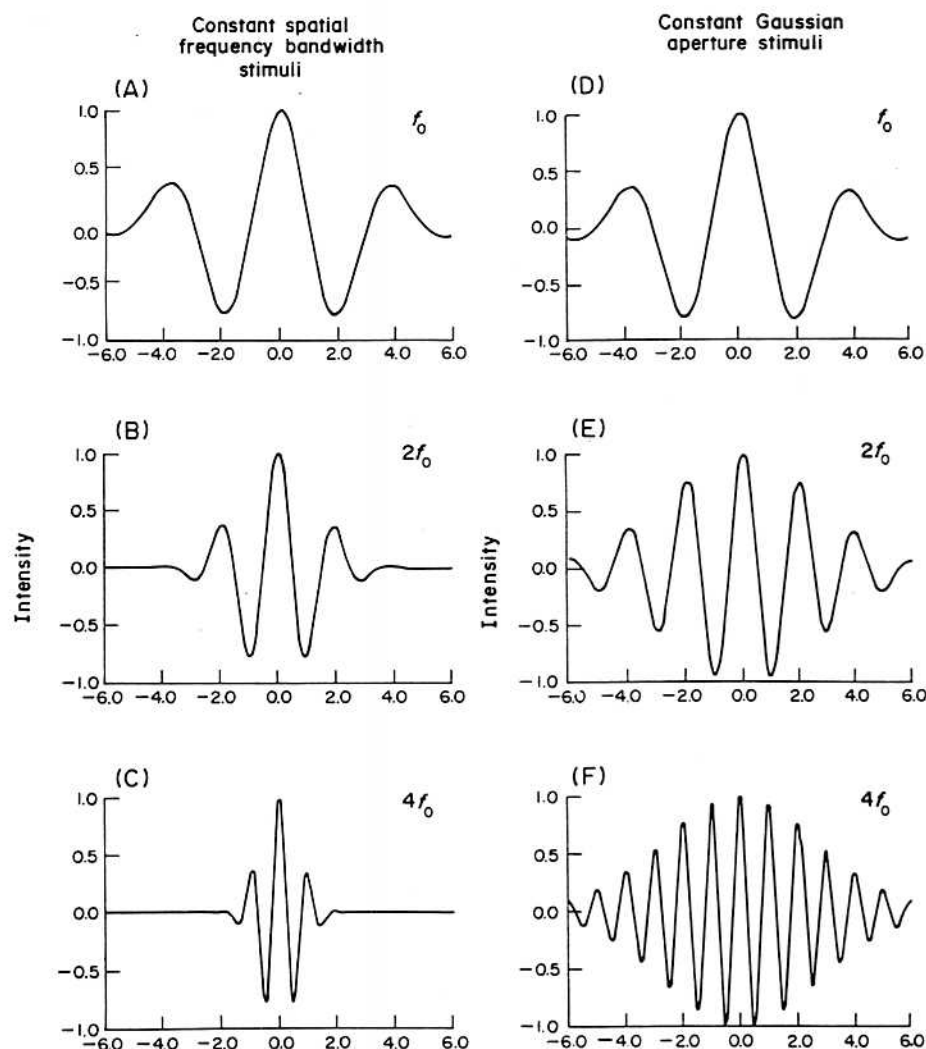


Fig. 1. (A–C) Profiles of “on center” even-symmetric Gabor stimuli in the constant bandwidth (in octaves) series are shown in order of increasing spatial frequency. The full bandwidths at  $1/e$  for each stimulus are one octave (or equivalently 0.8 octaves at half-amplitude), whereas the extent of the Gaussian envelope varies. (D–F) Gabor stimuli with constant Gaussian envelopes and varying bandwidths (in octaves) are shown in order of increasing spatial frequency. At the lowest spatial frequency the profile for the constant bandwidth series (A) and constant aperture series (D) are identical. At all higher spatial frequencies in the constant aperture series, the bandwidth is inversely proportional to the spatial frequency.

out estimates for orientation selectivity, the mean response/sec was averaged over the entire spatial response zone. Spatial frequency selectivity estimates in the constant relative bandwidth study were based upon evaluation of peak firing rates during a sweep of the stimulus, because the Gaussian envelopes were of different widths. However, in the constant aperture series, spatial frequency selectivity could be estimated either on the basis of peak firing rate or average response per sweep, because in this series the Gaussian envelopes were of identical spatial extents. All firing rates are presented as levels above the spontaneous activity.

## RESULTS

### *Responsivity of inferotemporal neurons*

Thirteen technically successful experiments were carried out in six monkeys. In 4 experiments, infer-

otemporal neurons failed to respond to any test stimuli, including the hands or faces of the experimenters, or habituated too rapidly for any meaningful measurements to be made. In the other 9 experiments, we obtained reliable data on 43 neurons. Of these, 31 responded long enough for determination of receptive field size and/or orientation selectivity before habituation precluded further quantitative study. Twelve neurons could be extensively studied quantitatively. Recording sites are shown in Fig. 2.

We confirmed the result of Gross *et al.* (1972) that the presence of slow waves in the EEG precluded a consistent response to visual stimuli. Nevertheless, the absence of pronounced slow waves in the EEG did not allow us to predict whether a given cell would habituate readily or not. Sometimes we could “arouse” a neuron transiently by preceding visual stimulation with a loud clap or stroking the fur of a forepaw. However, such transient periods of arousal

did not produce a stable enough baseline for quantitative studies.

When habituation occurred, it remained whether the stimulus tested was a drifting dark slit, a light slit, or a colored slit produced by using red, green, blue, or yellow filters. Attempts to circumvent the habituation process by interleaving stimuli at different orientations or by moving hands across the field between tests of the relevant stimuli proved futile.

#### *Receptive field sizes*

Most receptive fields had comparable lengths and widths. Width estimates were quantitatively determined from histogram measurements using long and narrow slits moving in the preferred direction. The receptive field profiles generally failed to show distinct subzones (Fig. 3A). There was no evidence for significant suppressive zones as the slit either approached or left the receptive field. Receptive field widths ranged from 8 to 43.6 deg. Receptive field widths of successive cells in a common penetration often varied by a factor close to two. The mean receptive field width for 26 cells was 15.7 deg and the median receptive field width was 16.6 deg. All fields included the central visual area within the accuracy of its localization, estimated as 1–2 deg.

#### *Orientation preferences and orientation selectivity*

Long and narrow ( $\sim 0.5^\circ$ ) drifting slits of light extending along the entire receptive field were first used to quantitatively test for orientation selectivity. Slit length was adjusted for maximal cell response. Cell responses increased with slit length until the full length of the field was reached. Such studies were usually done qualitatively, but in two cells quantitative studies were carried out. Response increased reasonably linearly with increase in slit length until

the field borders were reached and remained at maximal value after the field borders had been exceeded.

The half bandwidths at half-amplitude for orientation selectivity, as estimated for 10 cells ranged from  $9^\circ$  to  $45^\circ$ . Neurons separated in depth by less than  $200 \mu\text{M}$  might have very different half-bandwidths even though their orientation preferences were essentially identical (Fig. 4A–C).

After the orientation selectivity had been determined over the entire field, we subdivided the large receptive fields into four quadrants of approximately equal size and qualitatively tested the orientation selectivity within each quadrant. Given the propensity of these cells to habituate, we did not attempt to carry out detailed quantitative orientation studies in the four quadrants. However, in careful qualitative studies, we found no hint that the orientation preference or the directional preference within each quadrant was any different than it was for the entire field. Although minor differences of 10–15 deg in estimates of orientation selectivity within quadrants might have been missed, greater discrepancies are unlikely.

#### *Spatial frequency studies using Gabor stimuli*

Quantitative studies using Gabor stimuli were completed for eight cells in five different experiments. The high density of the data obtained, their reproducibility in repeated trials within each cell and the fact that results of the same type were found in all eight cells so studied suggests a high level of reliability for these results.

Responses of an inferotemporal neuron to the two types of Gabor stimuli (Fig. 1) are shown (Fig. 3). The responses to the Gabor stimuli of constant bandwidth are shown on the left (Fig. 3B–I) and the responses to the stimuli of constant Gaussian aper-

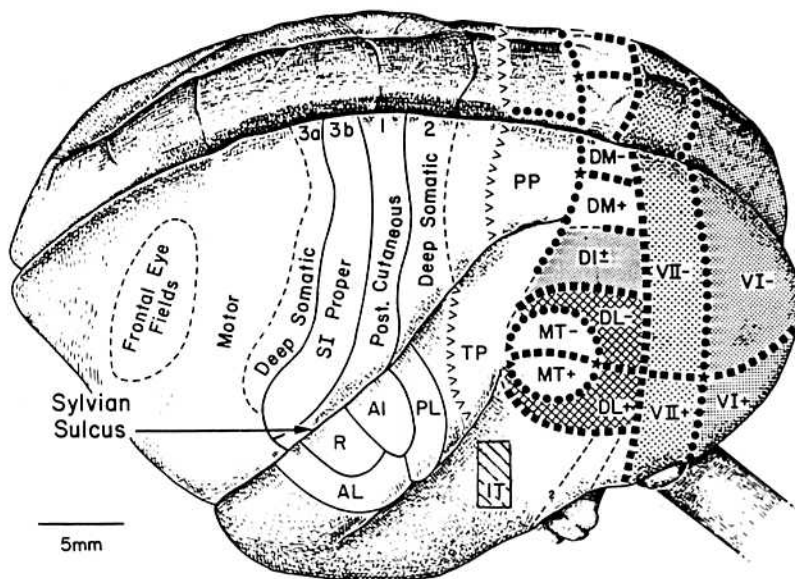


Fig. 2. Lateral view of cortex of owl monkey as modified and used with permission from Allman, 1982. The cross-hatched rectangular area in IT represents the region from which we have recorded.

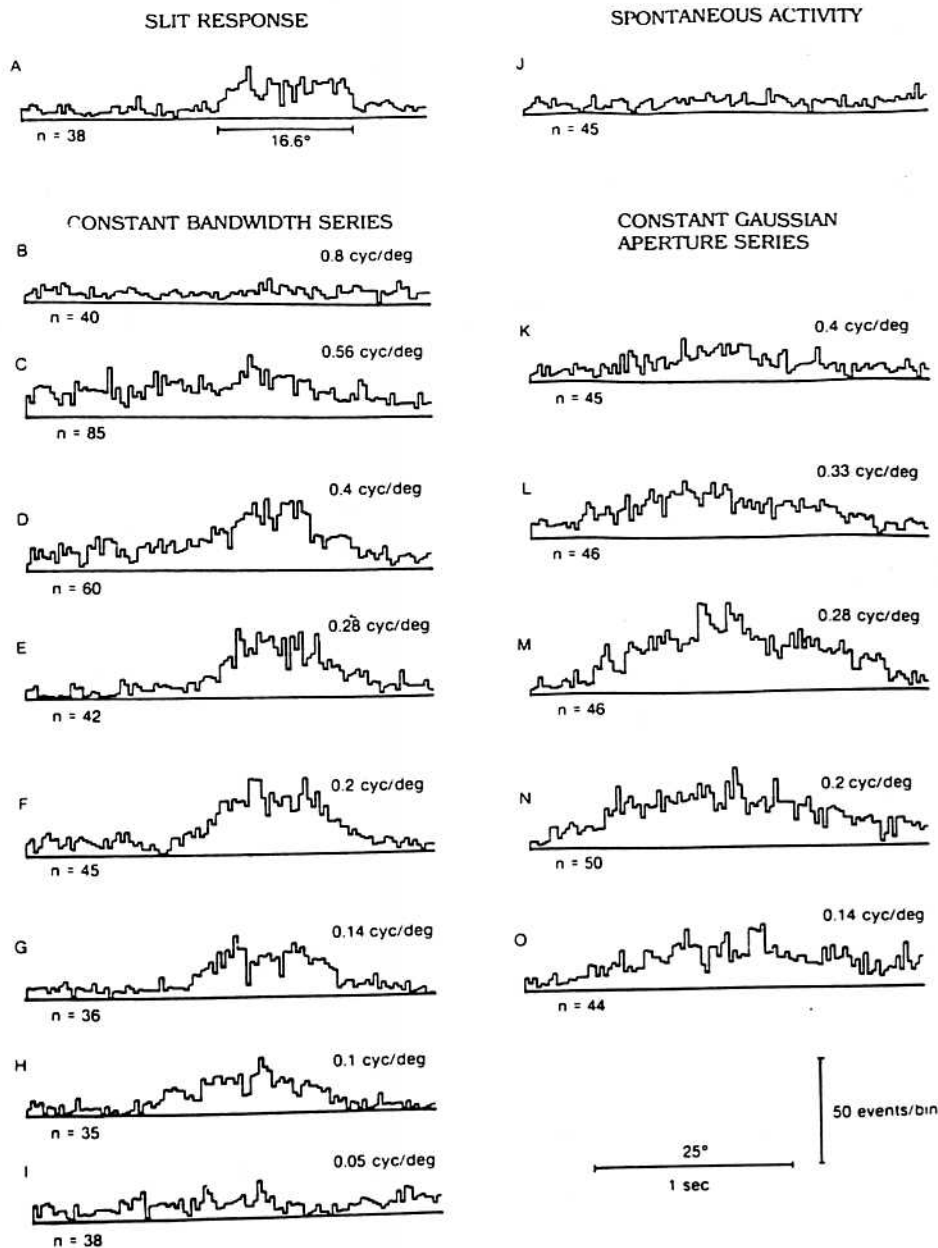


Fig. 3. (A) Average response histogram of an inferotemporal neuron to a narrow slit of light at the preferred orientation drifting across the receptive field. (B–J) Responses of same neuron to Gabor stimuli of constant bandwidth (in octaves) drifting across the receptive field in order of decreasing spatial frequency. (K–O) Responses of the same neuron to Gabor stimuli of constant Gaussian aperture in order of decreasing spatial frequency.

ture are shown on the right (Fig. 3K–O). Gabor stimuli of constant bandwidth with center spatial frequencies up to 2 octaves higher than the highest frequency shown in Fig. 3(B) were also tested and failed to produce a detectable response.

The peak response of any given cell for all frequencies tested in the constant relative bandwidth series occurred at the same position within its receptive field. Thus, there was no evidence either from this study or from the other seven studies that different spatial frequency bands produced selective responses in different parts of the receptive field.

The preceding results do not preclude the possibility that more than one spatial frequency band

projects to common loci within the receptive field. This possibility was examined by plotting the peak response vs the nominal spatial frequency tested (Fig. 4D–F). The spatial frequency selectivity curves for the Gabor stimuli of constant bandwidth (open circles) show that peak values occurred at only one spatial frequency and that there was only one peak for each cell. These results indicate that the receptive field receives input from only one spatial frequency band under these experimental conditions.

Peak responses of neurons to the Gabor stimuli from the constant relative bandwidth series at the preferred spatial frequency were substantial. Spontaneous firing rates usually ranged from 2 to 12 re-

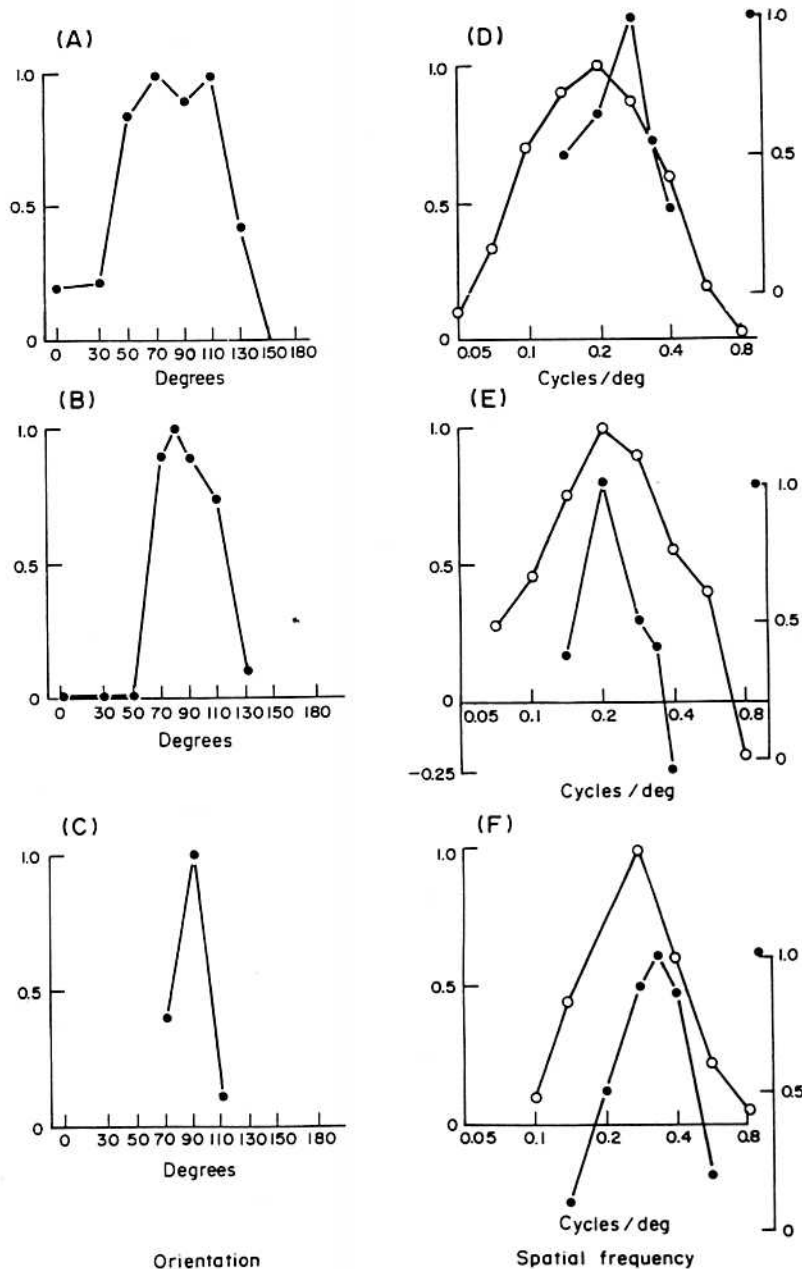


Fig. 4. (A–C) Orientation selectivity curves using a slit as stimulus for three neurons successively encountered in a single penetration. Records from cells 18-1, 18-2, and 18-3 respectively. (D–F) Curves for “spatial frequency” selectivity for three neurons in response to the Gabor stimuli of constant bandwidth (octaves) are indicated by open circles. The spatial frequency selectivity curves obtained when stimuli of constant Gaussian aperture are used are indicated by solid circles. Records from same three cells listed above respectively.

sponses per second. Peak firing rates of 35–40 spikes/sec above the spontaneous firing rate were not unusual and two cells responded at peak rates as high as 70–77 responses/sec (Table 1).

The preferred spatial frequency for neurons tested with Gabor stimuli of constant relative bandwidth ranged from 0.2 to 0.6 c/deg. These spatial frequencies fall at the very low end of the spatial frequency selectivity curve of the owl monkey (Jacobs, 1977). The high spatial frequency cut-off for some inferotemporal neurons extended up to 1.0 c/deg.

The “bandwidth” for the tuning curves plotted with Gabor stimuli of constant bandwidth are shown in Table 1. These “bandwidths” were usually about two octaves. However, these figures do not represent the actual spatial frequency bandwidth either of the individual neurons or “subunits” projecting onto the inferotemporal field or of the entire inferotemporal field because of the broad bandwidths of the stimuli themselves. Assuming linearity, Nagler (1983) has estimated that the actual bandwidths of the subunits would have been about 0.2–0.3 octaves less than the measured “bandwidths” provided in Table 1. Thus,

the subunits would generally have bandwidths of 1.3–2.0 octaves.

Estimates for the spatial frequency selectivity over the entire receptive field are provided by the studies with Gabor stimuli of constant Gaussian aperture (Fig. 3K–O). The histograms show a gradual increase in response density as the stimulus, with increasing contrast, enters and then fully covers the receptive field and then the gradual decrease in the response as the stimulus leaves the field. The response pattern to these test stimuli is modulated by the Gaussian but is independent of the phase of the sinusoidal components. The spatial frequency tuning curves based on these studies are plotted in Fig. 4(D–F) (solid circles).

Three points are noted upon comparing the tuning curves derived from the constant Gaussian aperture series with those derived from the constant bandwidth series. First, the peak spatial frequencies revealed by the two methods are very similar (Fig. 4E, F) or differ at most by one-half octave (Fig. 4D). Second, the full bandwidths found in studies carried out with gratings of constant Gaussian aperture are substantially narrower than those found in studies with the gratings of constant bandwidths. Bandwidths estimated by this method range from 0.87 to 1.3 octaves (Table 1). Actual bandwidth for fully extended sinewave gratings would be predicted to be narrower by only 0.001 to 0.005 octaves (Nagler, 1983). Third, in six of seven cases, the peak response to the preferred stimulus from the constant aperture series was less or even considerably less than the peak response to the preferred constant bandwidth stimulus (Table 1).

The preferred spatial frequencies for the gratings from the constant Gaussian aperture series ranged from 0.2 to 0.6 c/deg degree. The minimum number of full cycles within the receptive field was then calculated by multiplying the receptive field width in degrees by the preferred spatial frequency. This number ranged from 3.3 to 7.2 in seven cases and was 12.2 for one cell (29-3) with an enormous receptive field (Table 1). The number of full cycles within the field is substantially greater than the number of full cycles across the receptive field found for most simple cells or complex cells in the striate cortex (Movshon *et al.*, 1978).

#### Monocular and binocular stimulation

Most cells, when they responded at all, responded reasonably well to either eye although the response was generally stronger when the images to the two eyes had been binocularly converged. In two experiments the horizontal disparity of one image relative to the other was shifted in 0.25 deg steps on either side of the position for binocular convergence up to about 2 deg in order to determine whether the response to a drifting slit favored different retinal disparities at different positions in the receptive field. However, this was not the case because the disparity

Table 1. Response properties, as indicated within the Table, are given for 8 inferotemporal neurons

Cell	Preferred orientation (deg)	Orientation tuning half-bandwidth (deg)	Receptive field width (deg)	Preferred spatial frequency constant bandwidth series (c/deg)		"Bandwidth" constant bandwidth series (octaves)		Preferred spatial frequency constant aperture series (c/deg)		"Bandwidth" constant aperture series (octaves)		Peak response constant bandwidth series (responses/sec)	Ratio peak amplitude constant aperture series: peak amplitude constant bandwidth series		Number of cycles/receptive field at preferred spatial frequency
				bandwidth	series	bandwidth	series	bandwidth	series	bandwidth	series				
17-1	0°	—	10.0°	0.4	—	2.3	—	0.2	—	1.3	—	33.7	—	4.0	
18-1	80°	43°	16.6°	0.28	—	1.97	—	0.2	—	0.87	—	31.4	1.14	3.3	
18-2	80–90°	28°	17.0°	0.2	—	1.52	—	0.2	—	1.26	—	41.0	0.9	3.4	
18-3	90°	14°	9.0°	0.48	—	1.76	—	0.4	—	Indeterminate	—	77.2	0.53	3.6	
18-4	90°	—	13.0°	0.4	—	2.0	—	—	—	Indeterminate	—	70.1	0.37	5.2	
19-2	50°	9°	8.6°	0.48	—	2.05	—	0.48	—	0.5*	—	44.9	0.8	4.1	
21-3	0°	—	12.0°	0.6	—	1.1	—	0.6	—	Indeterminate	—	40.9	0.53	7.2	
29-3	135°	—	43.6°	0.28	—	—	—	0.28	—	—	—	6.3	0.4	12.2	

\*Half-bandwidth on high frequency side.

setting which produced the largest response for the central part of the receptive field produced the largest response for all parts of the field.

## DISCUSSION

A major conclusion of the present study is that the majority of neurons in the inferotemporal cortex of the lightly anesthetized owl monkey do not respond well enough for quantitative study of receptive field properties, at least with the limited class of stimuli tested here. Nevertheless, during the course of the entire study, we obtained enough new results, some qualitative and some quantitative, some confirmatory of previous work in old world monkeys and some entirely new, to warrant detailed discussion.

### *I. Results which confirm previous work*

Our results on the sizes and location of receptive fields in the owl monkey are similar to those of Gross *et al.* (1972) in the macaque and suggest a functional similarity of this cortex in the two species. Furthermore, Gross *et al.* (1972) found that a stimulus which was "optimal" for one part of the field was optimal for other parts of the field as well. We confirm this result in the sense that the center frequency of the Gabor stimulus in the constant relative bandwidth series which elicited the strongest response in one part of the field was also the preferred Gabor stimulus for other parts of the field as well. Moreover, when Gross *et al.* (1972) tested slits of different widths, they found that a slit of  $1^\circ$  width was generally optimal. This width is close to that of the half-period of the Gabor stimuli found to be preferred in the constant relative bandwidth series. Finally, our studies with long and narrow slits drifting across the receptive field perpendicular to the preferred orientation provided an estimate for the receptive field width but failed to provide any evidence for a discrete receptive field substructure, in agreement with Gross *et al.* (1972).

The orientation selectivity studies also confirm previous studies (Gross *et al.*, 1972) that a considerable degree of orientation selectivity is present for many inferotemporal neurons. Additionally, we made quantitative estimates of orientation bandwidth. Some cells had half bandwidths at half-amplitude of  $9^\circ$ – $14^\circ$  and others, sometimes even those of adjacent neurons, were considerably broader ( $28^\circ$ – $43^\circ$ ).

### *II. General new results*

First, in careful qualitative testing, we found that the receptive field orientation preferences within quadrantic subdivisions of the receptive field were the same as the orientation preference for the entire field. Thus, for these inferotemporal neurons there is no evidence for inputs from more than one orientation band.

Second, receptive field sizes of adjacent neurons commonly differed by a factor close to two. Thus, the

spread in receptive field sizes for adjacent neurons first found at the level of the striate cortex (Hubel and Wiesel, 1962) remains a factor in functional organization as far central as the inferotemporal cortex.

Third, inferotemporal neurons frequently gave substantially stronger responses to stimuli presented to both eyes in binocular convergence than to either eye alone. This is not surprising given the powerful binocular inputs and disparity selectivity of neurons in precedent visual cortices (Poggio and Fischer, 1977). Moreover, a new result here, although one tested in only two cells, was that the retinal disparity setting which produced the largest response for a stimulus presented to the central part of the field produced the strongest response for presentation of the stimulus within all parts of the field. Thus, we have found no evidence that different parts of these large receptive fields are selectively tuned for different retinal disparities.

### *III. Results from studies using Gabor stimuli*

From the tests with Gabor elemental functions, we were not able to find any evidence that more than one spatial frequency band fed onto an inferotemporal cell either in different or common parts of the receptive field. These studies also suggest that inputs from many lower level neurons sensitive to a common spatial frequency band feed into a single inferotemporal neuron. When studies with extended gratings were carried out, the bandwidth for spatial frequency narrowed as might be expected, but the bandwidths were still only comparable to those in the lower range of those obtained for striate neurons (Maffei and Fiorentini, 1973; Movshon *et al.*, 1978; Andrews and Pollen, 1979; De Valois *et al.*, 1982).

The difference between the bandwidths found for the constant aperture stimulus and those for the constant bandwidth series were typically greater than could be predicted simply from the relative bandwidths of these stimuli (Nagler, 1983). This argues either for some phase coherence in the summation process, somewhere between the striate cortex and the inferotemporal cortex, or for subunits with more cycles present than those in the constant relative bandwidth series used here, or for both. Nevertheless, any phase coherence cannot be complete because the measured bandwidths were generally substantially larger than the ones predicted for the entirely phase coherent linear case (Nagler, 1983).

Peak responses to an extended grating of the preferred spatial frequency were usually less than to Gabor stimuli of the same frequency from the constant bandwidth series. Had the system been both linear and completely phase coherent, one would have expected the responses to the extended grating of the preferred spatial frequency to produce substantially greater responses than those produced by the wave packets. A phase incoherent addition of the inputs from adjacent subfields might explain the failure of the bandwidths to narrow to predicted



values but would not explain the decreased peak response. Perhaps suppressive surrounds around neurons at preceding levels of the visual system (Maffei and Fiorentini, 1976) and/or non-linear processing may contribute to our results.

We found only low spatial frequency inputs to these inferotemporal neurons. However, we cannot exclude the possibility that middle and high spatial frequency bands project to the inferotemporal cortex but could not be detected under our experimental conditions. Perhaps middle and high spatial frequencies project onto those neurons which habituated too rapidly to be studied in detail. Another possibility is that inferotemporal neurons require precisely specified combinations of inputs before the higher frequency bands can influence cell firing rate. These possibilities remain speculative. Resolution of these might require the use of alert behaving animals in which at least the frequent problem of rapid neural habituation may be overcome.

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