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Brain Research 731 (1996) 91–100

BRAIN RESEARCH

Research report

Stimulus-dependent oscillations in the cat visual cortex: differences between bar and grating stimuli

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Accepted 9 April 1996

Abstract

We have investigated the dependence of cortical oscillations on the type of visual stimulus. Single unit recordings were performed in areas 17 and 18 of the cat visual cortex. Among 217 cortical neurons oscillations in the frequency range of 22–102 Hz were found in 29 cells (13%). The proportion of oscillating cells was higher (16%) if both bar and grating stimuli were used to stimulate cortical neurons. It was found that gratings are more effective than bars in triggering oscillatory patterns in cortical cells. Among 21 oscillating cells which were stimulated with both bar and grating stimuli, oscillations evoked with gratings were found in 17 neurons (81%) while oscillations evoked with bar stimuli were triggered in 7 cells (33%). The distributions of oscillation frequencies were statistically different for oscillations evoked with bars and gratings. Frequencies of oscillations evoked with bars were in the lower and higher range than frequencies of oscillations evoked with gratings. In 3 cells (14%), rhythmic patterns could be evoked with both bar and grating stimuli. However, the oscillations were of different frequencies. No significant correlation was found between the strength of oscillations and firing rate of cortical neurons. Both simple and complex cells manifested the same dependence on stimulus type. However, complex cells mostly exhibited oscillations in the lower frequency range while simple cells did so when neurons were stimulated with bars. The results suggest that various classes of visual stimuli can be coded by a temporal pattern of cortical responses.

Keywords: Visual cortex; Cat; Oscillation; Vision

1. Introduction

Oscillations in the γ-frequency range (~ 20–90 Hz) revealed in neuronal visual cortical responses constitute a phenomenon which is still not fully understood in spite of intensive studies. The low percentage or scarcity of oscillations and their complex dependence on stimulus parameters make investigators perplexed about a functional role of oscillations in visual cortical processing. Studies with single unit recordings failed to show any relationships between, for example, ocularity and oscillatory discharge and between the strength of oscillations and contrast of visual stimuli [6]. Likewise no clear association was found between oscillatory behavior and mean firing rate of cortical neurons [2,6]. Other investigators did find that several stimulus properties (velocity preference, moving vs. stationary stimuli) influence the temporal pattern of the periodic activity [7]. However, in previous experiments little attention was paid to the relationship between stimulus type (bar vs. grating stimuli) and occurrence of oscillations. It was only noted in some studies that stimulus type does influence the temporal pattern of neuronal responses. For instance, Eckhorn and Obermueller [4] have revealed a different proportion of oscillating cells when neurons were stimulated with bar or grating stimuli. However, they did not use both stimuli to excite the same cell. The relationship between oscillations and stimulus type was noticed by Ghose and Freeman [6]. These authors have compared oscillatory behavior of visual cortical neurons while the cells were stimulated with both grating and bar stimuli. They focused their analysis on the coherence of applied visual stimuli rather than on the type of stimuli. As bar stimuli, they used a random sequence of flashed and stationary bright and dark bars presented at an array of positions centered on the receptive field. This mode of stimulation is analogous to stroboscopic light pulses, and constitutes an incoherent type of visual stimulation. In addition, cortical cells respond weakly to stationary light

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PII S0006-8993(96)00468-4

slits, while moving bars evoke much better excitatory discharges. To further investigate the question of dependence of oscillations on stimulus type we performed the present investigation in which two coherent targets, both bar and grating stimuli, were applied to stimulate the same cortical neuron.

2. Materials and methods

2.1. Animal preparation

Adult cats (2.5–3.5 kg) premedicated with Atravet (acepromazine maleate, 1 mg/kg, i.m.) and atropine sulfate (0.04 mg/kg, i.m.) were anaesthetized with ketamine hydrochloride (25 mg/kg, i.m.) prior to catheterisation of the forelimb vein and tracheotomy. Xylocaine (lidocaine hydrochloride, 2%) was injected at surgical sites, and xylocaine cream was applied to pressure points. Cats were placed in the stereotaxic apparatus, paralysed with gallamine triethiodide (Flaxedil, initial dose 40 mg and 10 mg/kg/h during the experiment, i.v.) and artificially ventilated with a mixture of gasses (N_2O/O_2, 70/30, supplemented with 0.5–1.0% halothane (Fluothane)) for the duration of the experiment. Flaxedil was delivered to the animal continuously in a mixture of 5% dextrose in lactated Ringer's solution. A heating pad was used to maintain the body temperature at 37.5°C. Electrocardiogram and expired CO_2 were monitored throughout the experiment. The end-tidal CO_2 partial pressure was kept constant between 28–30 mmHg by adjusting the rate and depth of respiration. The antibacterial agent Tribrissen (24%, 30 mg/kg per day, s.c.) and the antibiotic Penlong (0.2 ml, i.m.) were administered to the animal. Pupils were dilated with atropine sulfate (1%) and the nictitating membranes were contracted with phenylephrine hydrochloride (2.5%). Plano contact lenses with no artificial pupils were placed on the cat's eyes to prevent the cornea from drying. The loci of the areae centrales were inferred from the positions of the blind spots, which were ophthalmoscopically back-projected onto a translucent screen. In most cases the non-dominant eye was occluded.

2.2. Recording

Extracellular single unit activity in the cortex (Horsley-Clarke coordinates F = 0.0– – 6.0; L = 0.0–6.0) was recorded by a glass micropipette (tip diameter 1.5–3.0 μm) filled with a solution of sodium chloride (0.9%). After the microelectrode was inserted, the cortex was covered with warm agar (3–4% in saline) and wax. The neuronal action potentials were amplified and sent to a computer where they were recorded with 1 ms resolution for on-line and off-line analysis. Oblique electrode penetrations were made in areas 17 and 18. Small electrolytic lesions (4 mA, 4 s, tip negative) were made at two or more sites for a histological determination of electrode positions after the experiment.

2.3. Visual stimulation and data collection

After a single unit recording was obtained, the cell's receptive field was determined using a hand-held projector with a narrow slit of light projected on a translucent screen placed 57 cm from the cat's eyes. During these preliminary tests, qualitative properties such as dimensions, orientation and directional selectivity, ocular dominance and velocity preference were noted. The quantitative evaluation of cellular responses was achieved electronically with images generated on a cathode ray screen (Mitsubishi Electronics, an effective display area of 380 × 285 mm, with a refresh rate of 56 Hz) centered on the receptive field and synchronized with the data acquisition processes. Tests were carried out with stationary and moving bars and drifting sinusoidal gratings. Each stimulus condition usually consisted of a 4-s presentation for gratings, 5-s for moving bars and 0.2–0.3-s presentation for stationary flashing bars. During quantitative tests, visual stimuli were presented in blocks of interleaved trials. Each stimulus was typically presented seven to 50 times. During these runs, peristimulus time histograms (PSTHs) were accumulated. PSTHs were computed for time of analysis corresponding to the time of stimulus presentation. In most cases, stimuli were presented at 50 or 80% contrast and selected contrast remained constant throughout an experimental run. Stimuli were symmetrically expanded about the center of the classical receptive field. Spontaneous activity was tested with no stimulus presented for the same number of trials and under the same mean luminance as for tests with the appropriate stimulus.

2.4. Data analysis

Two methods were combined to analyse oscillations within responses of cortical cells: examination of autocorrelograms (ACRGs) and computing the fast Fourier transform (FFT) of the ACRGs [6].

The ACRGs were computed from spike trains accumulated during data acquisition. To examine rhythmic discharges of neural origin, shift predictors were computed by cross-correlating spike recordings shuffled by one or two stimulus presentations, and these were subtracted from the 'raw' ACRGs. Recognition of oscillatory pattern had to meet three criteria: (1) ACRGs had to have at least two periodically-spaced peaks on either side of 0; (2) the shuffled ACRGs had to show a total absence of modulation; (3) peaks in the 'raw − shuffled' ACRGs had to exceed the confidence limits calculated by the computer (by multiple independent shuffles of ACRGs) by a factor of two ($P = 95\%$). Computing of confidence limits allows to determine whether peaks in ACRGs are statistically significant. This type of analysis takes into account a

possible variability of occurrence of peaks in the ACRGs between successive trials.

The oscillation frequencies and oscillation strength were derived from the FFT histograms. The FFT analysis of ACRGs also served as a control for occurrence of oscillations in neuronal responses. All measurements were performed on the 'raw − shuffled' ACRGs. Calculations performed on the 'raw − shuffled' ACRGs allowed to quantitatively measure oscillation strength with noise subtracted [6]. The ACRGs (bin width 1 ms) were reflected to span intervals from −256 to +256 ms before the Fourier transform. For FFT histograms, noise was estimated by averaging the power between 250 and 500 Hz. Peaks in the FFT histograms were considered to be significant if signal/noise ratios exceeded 1.5 [6].

Cells were classified as simple or complex according to criteria based on those of Hubel and Wiesel [11]. The classification was also confirmed by using grating stimuli. FFT analysis of PSTHs was performed to calculate AC/DC ratios in responses of cortical neurons. Cells for which AC/DC ratio exceeded 1.0 were considered to be simple while cells with AC/DC ratio less than 1.0 were classified as complex [17].

2.5. Histology

At the end of the experiment, the animal was deeply anaesthetized with Nembutal and perfused through the heart with saline and paraformaldehyde. The brain was removed and prepared for histology. Blocks of tissue containing the electrode tracks were sectioned on a freezing microtome. Every other section of the cortex was prepared for Cresyl Violet staining to define the position of the microelectrode in cortical areas 17 and 18.

3. Results

3.1. Categorising neuronal responses as oscillatory

As indicated above, unitary responses were identified as either oscillatory or nonoscillatory if three criteria were met when ACRGs of neuronal discharges were examined. A power spectrum analysis shows that if ACRGs do not contain at least two periodically spaced peaks on either side of 0 FFT histograms also fail to exhibit a discernable peak at any frequency with a power value higher than the

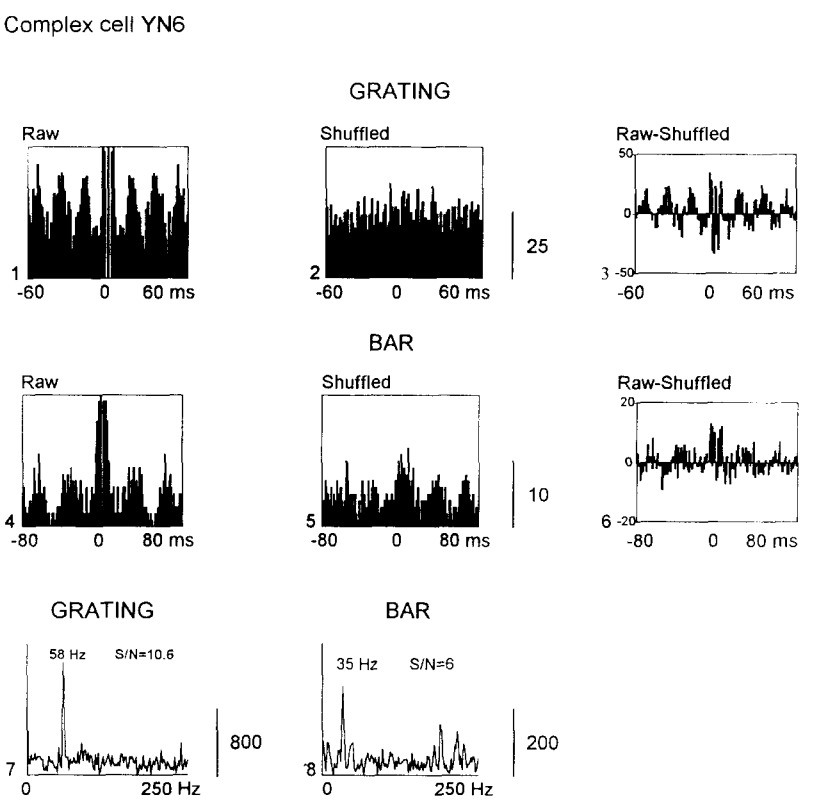

Fig. 1. Categorising neuronal oscillations. Complex cell YN6 manifested oscillations at ~ 58 Hz to gratings of optimal parameters (0.2 c/d, 2 Hz, 10 × 10°) (autocorrelograms (ACRGs) of Traces 1 and 3 and FFT histograms of Trace 7). The shuffled ACRG showed no modulation (Trace 2) indicating the neural origin of oscillations. Stationary flashing light slits (0.2 s, 0.5 × 10°) evoked in the same cell a 35 Hz rhythmic pattern (Traces 4, 6 and 8). However, the shuffled ACRG (Trace 5) demonstrated modulation in this case. Though the oscillations 35 Hz were not at the refresh rate of the stimulus CRT the cell was categorised as oscillating for grating but not for bar stimuli. For this figure and Figs. 2 and 3 calibration: spikes/bin, bin width 1.95 Hz for FFT histograms.

average value of the noise. Our computations indicated that if peaks in ACRGs were estimated as significant by calculating the confidence limits then the signal/noise ratio of the peak in the power spectrum exceeded 1.5. This value corresponds to the criterium adopted by Ghose and Freeman [6] for classifying cells as oscillatory. Another important point for identifying an oscillatory neuron is the absence of any modulation in the shuffled ACRGs. This procedure eliminates the possibility that oscillations are due to a screen refresh rate and consequently to establish that the rhythmicity within responses are of neuronal origin. It is important to mention that in some cells responses exhibited oscillations at different frequencies to bars and gratings, and shuffling ACRGs were unsuccessful to suppress oscillations to one of the stimuli. In this case if oscillations were present in the shuffled ACRGs for one type of visual stimulation the cells were classified as nonoscillating for this type of stimulus but oscillating for another type of stimulus for which no modulation was recorded in the shuffled ACRGs.

Fig. 1 demonstrates one example of oscillations present within evoked responses. A complex cell YN6 (AC/DC =

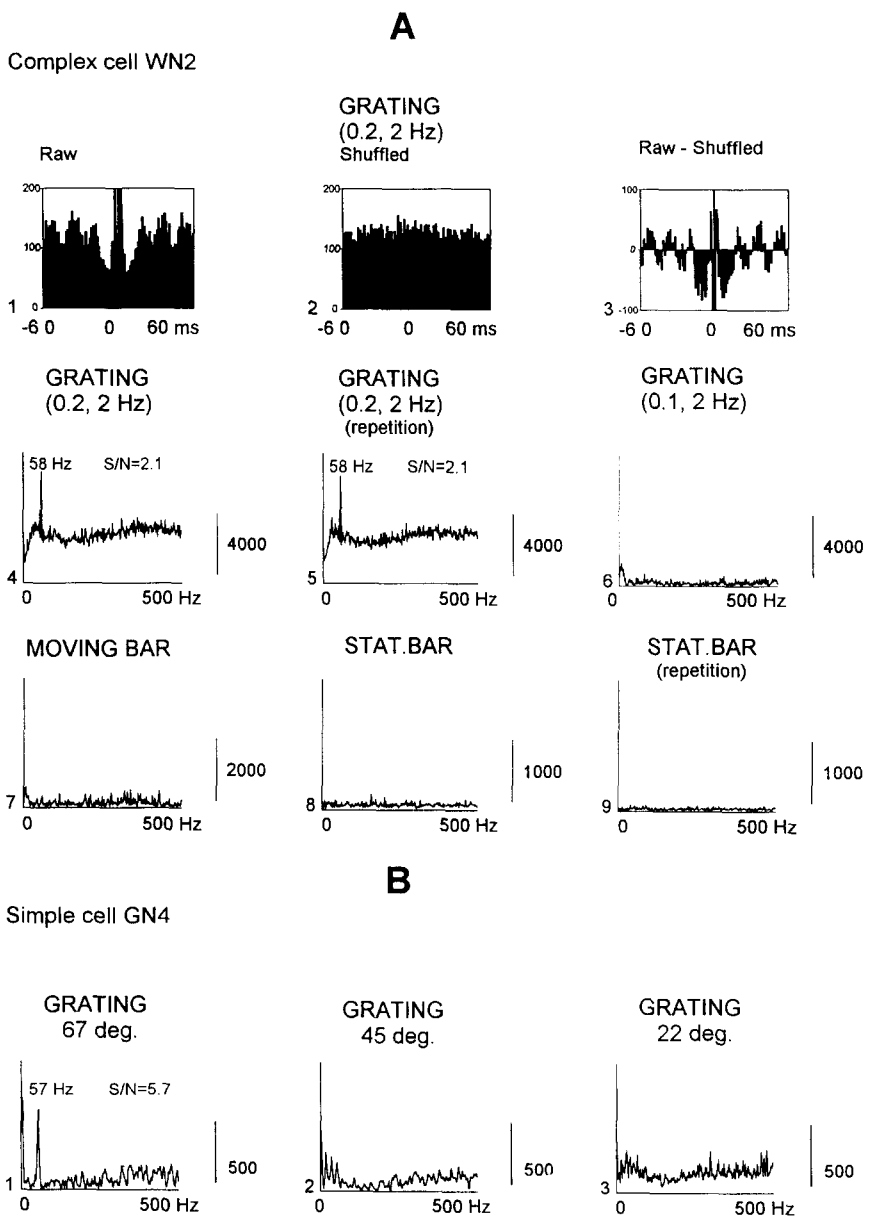

Fig. 2. Stimulus dependence of cortical oscillations. A: complex cell WN2 exhibited a clear rhythmic pattern ~ 58 Hz only to gratings of optimal parameters (0.2 c/d, 2 Hz) (autocorrelograms (ACRGs) of Traces 1 and 3 and FFT histograms of Traces 4 and 5) while the same stimulus but of another spatial frequency did not evoke oscillations (Trace 6). Moving ($0.5 \times 40°$, 4°/s) and stationary flashing ($0.5 \times 40°$) light slits were not effective in producing oscillations in this cell (Traces 7–9). Note also that no modulation is seen in the shuffled ACRG (Trace 2) that indicates that oscillations were of neural origin. B: simple cell GN4 exhibited oscillations ~ 57 Hz only to gratings of optimal orientation (Trace 1) (the 'raw − shuffled' ACRG for this cell is shown in Fig. 3). Gratings of other orientations (Traces 2 and 3) presented on the same monitor did not disclose rhythmic patterns.

Table 1
Proportion of oscillating cells depending on stimulus type

	Area 17		Area 18		Total
	Simple	Complex	Simple	Complex	
Bar	8.7% (4/46)	5.2% (3/58)	8.3% (4/48)	4.1% (2/49)	6.5% (13/201)
Grating	12.2% (5/41)	9.8% (4/41)	17.6% (6/34)	14.3% (4/28)	13.2% (19/144)
Bar + Grating [a,b]	11.1% (4/36)	16.7% (6/36)	22.6% (7/31)	16.0% (4/25)	16.4% (21/128)
Total [b]	15.7% (8/51)	11.1% (7/63)	15.7% (8/51)	11.5% (6/52)	13.4% (29/217)

[a] Subset of the population (cells tested with both bar and gratings).
[b] The 3 cells which oscillated with both bar and grating stimuli are counted once.

0.8) showed clear oscillations at ~ 58 Hz in its responses to grating stimuli (signal/noise = 10.6) (Traces 1 and 7). The modulation was absent in the shuffled ACRG (Trace 2). The neuron oscillated with another frequency (~ 35 Hz) to presentation of a light bar (Traces 4 and 8). However, modulation was seen in the shuffled ACRG (Trace 5). In keeping with our criteria, the cell was classified as oscillatory only to grating stimuli.

Another typical example is displayed in Fig. 2. Oscillations at ~ 58 Hz in the evoked discharge of the complex

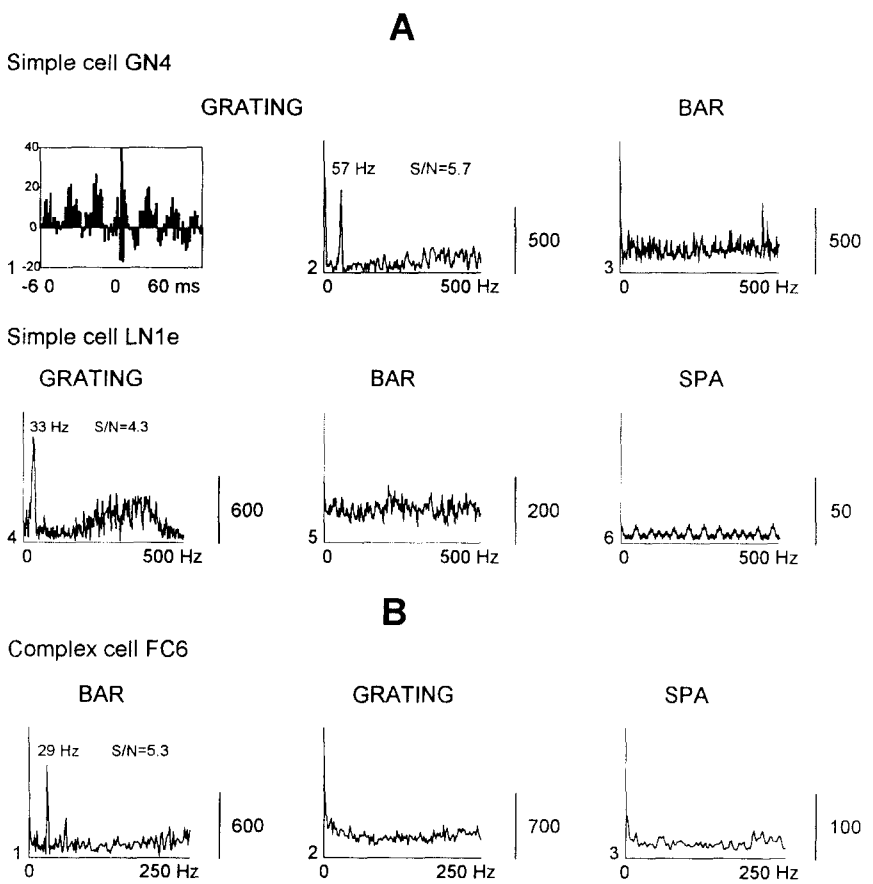

Fig. 3. Stimulus specificity of cortical oscillations. FFT histograms computed from the 'raw − shuffled' autocorrelograms (ACRGs) are shown. A: in this case, only gratings of optimal parameters were effective to provoke oscillatory patterns in responses of these two cells. Gratings and bars were of the same orientation and direction. Stimuli for a simple cell GN4: gratings (0.1 c/d, 28.5 × 38°) drifting with a temporal frequency 2 Hz (6 presentations of the stimulus for Traces 1 and 2) and light slits (0.5 × 40°) moving with a velocity 4°/s (7 presentations of the stimulus for Trace 3). Trace 1: the 'raw − shuffled' ACRG. Simple cell LN1e was stimulated with gratings (0.1 c/d, 28.5 × 38°) drifting with a temporal frequency of 2 Hz (Trace 4, 30 presentations of the stimulus) and light slits (0.5 × 6°) moving with a velocity 8°/s (Trace 5, 30 presentations of the stimulus). Spontaneous activity (SPA) was recorded for the same time as for gratings. B: FFT histograms are shown for a cortical cell for which only bars of optimal parameters were effective to evoke oscillatory patterns. Gratings and bars were of the same orientation and direction. Complex cell FC6 was stimulated with light slits (0.5 × 7°) moving with a velocity 8°/s (Trace 1, 7 presentations of the stimulus) and gratings (0.1 c/d, 28.5 × 38°) drifting with a temporal frequency of 2 Hz (Trace 2, 7 presentations of the stimulus). SPA was recorded for the same time as for gratings.

cell WN2 (AC/DC = 0.6) were prononced in both the 'raw' (Trace 1) and 'raw − shuffled' (Trace 3) ACRGs while the 'shuffled' ACRG showed no modulation (Trace 2). This indicates the neural origin of the rhythmic patterns. The oscillations were very stable and appeared with the same frequency and the same signal/noise ratio when a second presentation of the same stimulus was carried out (compare Traces 4 and 5; total number of spikes in PSTHs: 3253 and 3099, respectively). On the other hand, gratings of a non-optimal spatial frequency (Trace 6, total number of spikes in the PSTH: 1880) and moving or stationary flashing bars (Traces 7–9) failed to induce oscillations though they were presented on the same monitor.

The simple cell GN4 (AC/DC = 1.8) exhibited oscillations (~ 57 Hz) when it was stimulated with gratings of optimal orientation (Fig. 2B, Trace 1). Gratings of other orientations shown on the same monitor did not trigger the rhythmic pattern (Fig. 2B, Traces 2 and 3).

3.2. Probability of occurrence of oscillations depending on stimulus type

A total of 217 cortical cells were studied in our experiments (area 17/area 18: 114/103). Of these, 73 neurons were stimulated only with bars, and 16 cells were stimulated only with gratings. The remaining 128 cells were stimulated with both bars and gratings. Oscillations ~ 22–102 Hz were found in 13% of cells (area 17/area 18: 15/14) (Table 1).

The proportion of oscillating neurons was found to be dependent on the stimulus type. The relative proportion of rhythmic patterns encountered in cortical cells was higher with gratings (13%, 19 out of 144 cells) than with bars (6%, 13 out of 201 neurons). These data suggest that gratings are more effective in eliciting oscillatory patterns in cortical cells than bars. When both bars and gratings were employed to stimulate the same cell, the proportion increased up to 16% (21 out of 128 cells) (Table 1). This indicates that when bars and gratings are tested on the same unit the proportion of cells with oscillating pattern increases. In the following, we present results for these 21 cells which were stimulated with both bars and gratings and which showed rhythmic patterns in their responses.

3.3. Dependence of occurrence of oscillations on the type of visual stimuli

Results show that occurrence of cortical oscillations is highly dependent on the type of visual stimuli employed to excite the neuron. Among 21 oscillating cells stimulated with both bars and gratings, oscillations evoked with gratings were found in 17 neurons (81%) while oscillations evoked with bar stimuli were triggered in 7 cells (33%). It should be emphasised that oscillations were not seen in the spontaneous activity of all these cells. We observed only one cell which exhibited a rhythmic pattern in its spontaneous activity and this neuron was excluded from further analysis.

Fig. 3 demonstrates several examples of oscillations specifically related to the sort of visual stimuli. Simple cell GN4 shown in Fig. 3A exhibited rhythmic patterns of ~ 57 Hz only to gratings of optimal parameters (Traces 1 and 2) and did not show any oscillatory activity in the frequency range of 20–100 Hz while it was stimulated with moving light slits (Trace 3). Note, however, that light bar evoked a peak in the FFT histogram in the higher frequency range (449 Hz in this case). Peaks at the same high frequency in responses to bars were also seen in two other cells (CN1 and EN2) in which oscillatory activity was evoked only with grating stimuli. These high frequency peaks presumably indicate the occurrence of equal interspike intervals in the responses of these neurons to bar stimuli. Fig. 3A exhibits additional dependence of the rate of occurrence of oscillations on the kind of visual stimuli for another unit (LN1e). A clear peak at ~ 33 Hz in the FFT histogram emerged in the response of this simple cell (AC/DC ratio = 2.4) only when the neuron was stimulated with gratings of optimal parameters (Trace 4). The oscillations were not seen in the spontaneous activity of this cell (Trace 6) and did not appear when the neuron was stimulated with moving bars of the same direction and orientation (Trace 5).

Fig. 3B provides one example where only bars of optimal parameters were effective in evoking oscillatory patterns. This complex cell FC6 (AC/DC = 0.7) exhibited a rhythmic pattern ~ 29 Hz in response to moving light slits (Fig. 3B, Trace 1). Interestingly, no oscillations were seen in response to gratings (Fig. 3B, Trace 2). No rhythmic pattern in spontaneous activity of this neuron was apparent (Fig. 3B, Trace 3).

Fig. 4 displays the overall distribution of oscillation frequencies and signal/noise ratios plotted for all 21 cells. The range of frequencies for oscillations elicited with gratings is between 22 and 102 Hz while the range is between 29 and 96 Hz for oscillations evoked with bars. The corresponding mean values (mean ± S.E.M.) for gratings were 54.5 ± 4.5, and for bars: 57.2 ± 10.6. Frequencies of oscillations evoked with bars are generally at both extremes of the spectrum. The distribution of oscillation frequencies (Fig. 4A) is statistically different for oscillations evoked with bar and grating stimuli (Kolmogorov-Smirnov two-sample test, $\chi^2 = 3.09$, $df = 2$, two-tailed $P = 0.4$). On the other hand, the distribution of signal/noise ratios shows no clear difference in values of signal/noise ratios between bars and gratings (mean values (mean ± S.E.M.) for gratings 3.5 ± 0.6, for bars: 2.7 ± 0.5).

For three cells out of 21 (14%), oscillations could be evoked with both bar and grating stimuli. However, the oscillations were of different frequencies. For two neurons, there was little difference between the corresponding values for bars and gratings (cell JN2: 74 Hz for gratings and

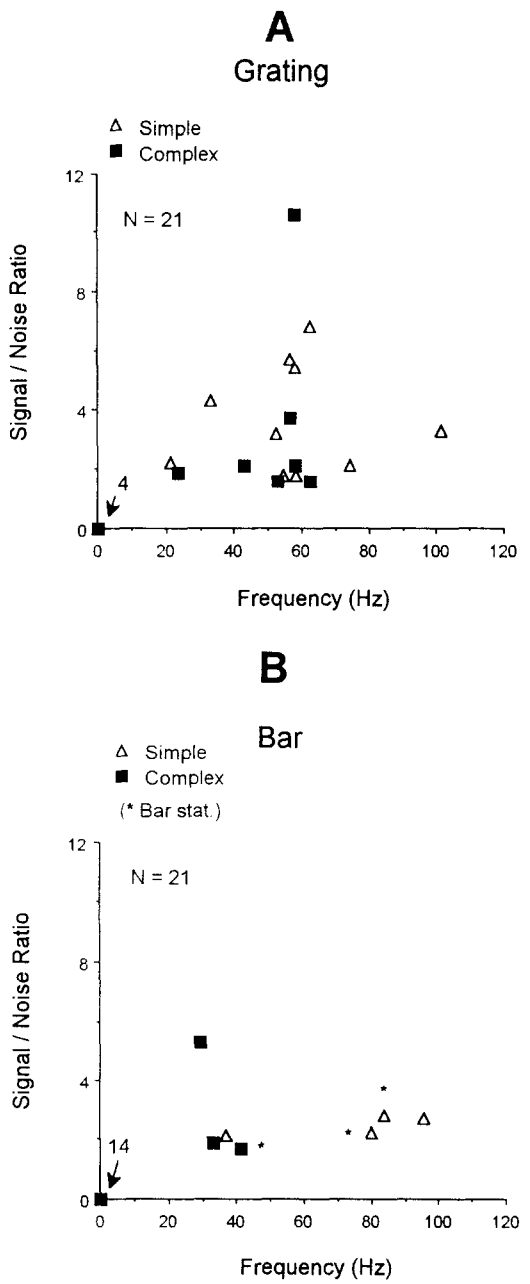

Fig. 4. Plots of oscillation frequencies as a function of signal/noise ratios. A: oscillations were evoked with grating stimuli. B: oscillations were evoked with bar stimuli.

80 Hz for bars, cell JN1: 102 Hz for gratings and 96 Hz for bars). For the third cell FC1, the difference was significant (53 Hz for gratings and 37 Hz for bars). It may suggest that the form of the target also changes the frequency of oscillations of a single neuron.

3.4. The occurrence of oscillations and cell type

Among 128 neurons which were stimulated with both bar and grating stimuli, oscillations were found in the same proportion for both physiological cell types (16%, or 11 out of 67, simple cells and 16%, or 10 out of 61, complex cells). Out of 21 analyzed neurons which exhibited oscillations, 11 (52%) were simple cells and 10 (48%) were complex cells. Oscillations evoked with gratings were found in 10 simple cells and 7 complex cells. Bar stimuli triggered rhythmic patterns in the responses of 4 simple cells and 3 complex cells. The clustering of oscillation frequencies in responses to gratings around 60 Hz was typical for both cell types (Fig. 4A). However, complex cells mostly exhibited oscillations in the lower frequency range than simple cells did when neurons were stimulated with bars (Fig. 4B). Both simple and complex cells exhibited the same dependence on stimulus type as was demonstrated in Figs. 1–3.

3.5. The strength of oscillations

Another question which deserves attention is the relationship between the strength of the responses and the strength of oscillations. This relationship is analyzed in Fig. 5. It seems clear that for simple and complex cells and for both modes of stimulation there is no significant trend between the discharge rate and the magnitude of oscillations ($\alpha = 0.5$, N.S.). The results may indicate that the firing rate and the rhythmicity are generated through independent processes.

4. Discussion

We have investigated the dependence of cortical oscillations on the type of visual stimuli. Single cell spike trains were analyzed for occurrence of rhythmic patterns in responses of cortical neurons. Oscillations in the frequency range of 22–102 Hz were found in 13% of cortical cells. However, the proportion of oscillating neurons was found to be dependent on the stimulus type. To our knowledge, the comparison of proportions of oscillation occurrence as a function of stimulus type (bars vs. gratings) has not previously been investigated.

4.1. Technical considerations

It was noted that the dominant frequencies of oscillations evoked with gratings were clustered in our experiments around ~60 Hz (mean ± S.E.M.: 54.5 ± 4.5 Hz). To rule out a contamination of a refresh rate of the screen we performed a shuffling of all ACRGs. This operation failed to disclose any modulation in the shuffled ACRGs. In addition, all our measurements were made on the shuffle-subtracted ACRGs. Thus it may be concluded that oscillations revealed in our experiments were of neural origin. Furthermore, we used visual stimuli of different parameters which revealed that oscillations correlated with optimal parameters of stimulating targets (Fig. 4). For example, gratings of slightly different (non-optimal) spatial frequencies did not trigger oscillations though these grat-

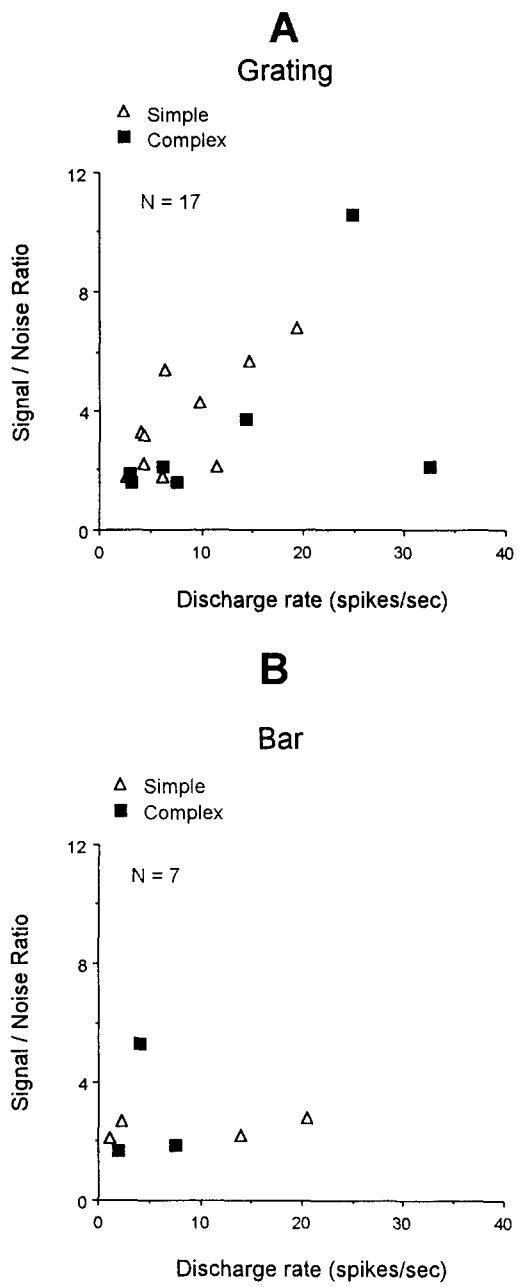

Fig. 5. Signal/noise ratio is plotted vs. mean discharge rate of cortical cells. No clear relationship between both parameters was found. A: oscillations were evoked with grating stimuli. B: oscillations were evoked with bar stimuli.

ing stimuli were presented on the same monitor with the same refresh rate. In a separate study [15] we have shown that deactivating the pulvinar complex with microinjections of GABA reduces or even abolishes the cortical stimulus-dependent oscillations. This result is difficult to reconcile with the proposal that the refresh rate of the monitor is generating the oscillatory pattern. Indeed, if oscillations were due to monitor's refresh rate they should not be affected by pulvinar injections. Finally, oscillation frequencies were different for bar and grating stimuli for the same cell. Along this line, it is important to compare these results with data of other investigators who used CRT with a different refresh rate. Data are available from the study of Ghose and Freeman [6]. Although the refresh rate of their monitor was 76 Hz the authors reported a large proportion of neurons oscillating at frequencies near 60 Hz. They also noted that oscillations at frequency around 76 Hz were not prevalent and that only 3% of all oscillations observed were at frequencies > 63 Hz. This is in accordance with the present results.

4.2. Comparison of frequency ranges

Oscillation frequencies calculated in our experiments extended from 22 to 102 Hz. This range is in agreement with previous studies [3,4,6,9]. Interestingly, the frequency range in our experiments differed significantly between bar and grating stimuli. Cells oscillating to gratings exhibited oscillations with dominant frequencies near 60 Hz. Frequencies of oscillations evoked with bars were, as a rule, in the lower and higher range than frequencies of oscillations evoked with gratings. It was particularly evident for neurons which exhibited rhythmic patterns to both bar and grating stimuli. Different oscillation frequencies for bars and gratings were also reported by Ghose and Freeman [6]. The authors, however, reported that 56% of cells which exhibited oscillations to incoherent stimulation (set of flashing bars) did it at higher frequencies than with coherent (gratings) stimulation.

4.3. Stimulus dependence and scarcity

The present investigation shows that gratings are more effective than bars in triggering oscillatory patterns in cortical cells. Only 6% of neurons in our study exhibited rhythmic patterns if only bars were employed to stimulate cortical cells. This proportion is lower than the one reported by Gray et al. [7]. They have found 27% of oscillating cells using bars as visual stimuli. The lower percentage of occurrence of oscillations in our study could be explained by different methods of categorising oscillations. If only gratings were employed to stimulate cortical cells the proportion of oscillating neurons in our experiments increased up to 13%. When both bar and grating stimuli were used oscillatory behavior was found in 16% of units. The latter value is comparable to the percentages reported elsewhere.

In all studies the relative proportion of cells which exhibit oscillations within their evoked firing pattern is relatively small (20–25%: [2,7]). This weak proportion cannot be attributed to technical difficulties in evaluating rhythmic firing because the same technique applied to multiunit recordings is reported to disclose a higher proportion (> 60%) of oscillatory responses (e.g. [8]). A larger proportion of oscillatory responses in multiunit activity might arise because of recording simultaneously

from a large population of neurons which include some cells exhibiting rhythmic firing.

However, a relative scarcity of oscillations may stem from a genuinely general physiological principle. Indeed, if we assume that oscillations are implicated in synchronising the firing of cortical neurons that are activated by specific trigger features of a single target, then one can expect a low occurrence of oscillations. The implication of the above statement is that neurons must be presented with a coherent image which will make the cell fire in a rhythmic fashion. But from a cellular stand point how can coherence be defined? This notion is difficult to define at the present time; however, the necessity of cohesion requires very stringent conditions to be applied to the stimuli, because each particular image (or a part of it) must contain all attributes that make it coherent in regard to cellular activity. Given the above difficulty and experimental constrains it is not surprising that recording oscillatory activity is a relatively rare occurrence, particularly if recordings are done at single cell level. Conversely, if oscillations were widely spread then one may argue that their functional significance is associated with some general level of excitability which would be unrelated to the specificity or the characteristics of the targets.

We employed a large set of visual stimuli in our experiments. Although the proportion of disclosed oscillating cells was low, we have the impression that, had we, with others, found the 'pertinent' stimulus or the appropriate conditions, the proportion of cells responding with stimulus-dependent oscillations would have increased. That is, it seems that some type of stimuli will generate rhythmic activity while other modes of stimulation appear to be inefficient in producing oscillations.

4.4. Dual mode of activity

Our results suggest that discharge rate and oscillation strength are unrelated. This absence of relationship suggests that cellular mechanisms which generate each mode of activity are independent of each other. This should not be surprising because many intracellular recordings of cortical cells have shown that oscillations of membrane potentials depend upon the level of resting membrane potentials prior to the moment of stimulus application. For instance, neurons of the thalamo-cortical circuits exhibit a firing pattern which depends upon the membrane potential of the cortical or thalamic cell. In vivo studies show that depolarization makes the unit fire at 10 Hz while a small hyperpolarization fires the same cell at 6 Hz. Thus thalamic cells have dual firing levels [12,18]. In the neocortex, it has been shown that, in some pyramidal cells, the unit may undergo a repetitive activation of the NMDA-receptor mediating pyramidal-pyramidal neuron synapses when the membrane potential is less negative than −70 mV. This 'self-facilitation' may develop in entraining a cellular network in a rhythmic activity [19].

4.5. Concluding remarks

The stimulus dependency of cortical oscillations is still under debate. The results of different investigators appear to be contradictory. Our study shows that cortical oscillations manifest a clear dependency on the stimulus type. It is known that both bar and grating stimuli are optimal to trigger cortical responses. From the classical point of view, cortical neurons can be characterized as detectors of lines or edges of definite orientations [10,11]. Another hypothesis proposes that cortical cells are not detectors of lines but spatial-frequency filters which may analyze the world into spatial frequency components [13]. Though both hypotheses are in use at the present time it was noticed by investigators that cortical cells often respond more vigorously to gratings than to bar stimuli [1]. Along this line, our results confirm that gratings are more effective than bars in provoking oscillations in cortical neurons. The hypothesis of temporal coding of information [14,16] suggests that object representation in the visual cortex is achieved by synchronous activity of assemblies of cortical neurons responding to features of the same object. From this point of view, oscillatory signals may be well suited as carrier signals for a temporal code [5]. Dependency of oscillations on the stimulus type shown in the present investigation seems to support this hypothesis as stimulus type can be coded by a temporal pattern of cortical responses.

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