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Oscillatory Discharge in the Visual System: Does it Have a Functional Role?

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SUMMARY AND CONCLUSIONS

1. The discharge of individual neurons in the visual cortex and lateral geniculate nucleus (LGN) of anesthetized and paralyzed cats and kittens was examined for the presence of oscillatory activity. Neural firing was evoked through the monoptic or dichoptic presentation of drifting gratings and random sequences of flashed bars. The degree to which different oscillatory frequencies were present in neural discharge was quantified by computation of the power spectra of impulse train responses.

2. Action potentials from single cells were recorded extracellularly and isolated on the basis of amplitude. Receptive-field properties of the neurons under study were characterized initially by their discharge in response to gratings of sinusoidal luminance. By varying orientation and spatial frequency, optimal stimulus characteristics were determined. Oscillation analysis was performed on spike trains acquired during repeated presentations of the optimal stimulus by identification of power spectra peaks in the frequency range of rhythmic potentials observed in electroencephalograph studies (30–80 Hz). The amplitude and frequency of the largest peak in this range was used to characterize oscillatory strength and frequency. All discharge in which the peak amplitude exceeded the high-frequency noise by a factor >1.5 was classified as oscillatory.

3. Of the 342 cortical cells examined, 147 cells displayed oscillatory activity in the 30 to 80-Hz range during portions of their visual response. Sixty out of 169 simple cells, 82 out of 166 complex cells, and 5 out of 7 special complex cells exhibited oscillations. There was no laminar bias in the distribution of oscillatory cells; the proportions of oscillatory cells were similar in all layers. All oscillatory discharge was variable with respect to frequency and strength between successive presentations of the same optimal stimulus. In as little as 10 s, for example, peak frequencies shifted by a factor of two. For many cells, these trial-to-trial variations obscured detectable oscillations when all trials were averaged together.

4. The potential role of neuronal maturation in the generation of oscillatory activity was investigated by studying neuronal responses from kittens at 4 wk postnatal. Of the 80 kitten cells studied, 27 exhibited oscillatory discharge. Although oscillations in the kitten visual cortex spanned the same frequency range as that seen in the adult, oscillations in the midfrequency range (36–44 Hz) are more common in the adult cortex.

5. To explore the possibility that oscillations might play a functional role in vision, we investigated the dependence of oscillations on different stimulus parameters. Responses to dichoptically presented drifting gratings showed no relationship between binocular interactions and oscillatory discharge: oscillations were just as likely to occur with nonoptimal as with optimal binocular stimuli. For 98 binocular cells that exhibited oscillatory discharge, monocular and binocular responses were compared. Sixty-one of these cells exhibited oscillatory discharge under both monocular and binocular stimulation. The numbers of cells that oscillated solely under binocular stimulation or solely under monocular stimulation were approximately equal (18 and 19, respectively). Among the 61 cells that oscillated with both monocular and binocular stimuli, about one-half showed stronger oscillations for binocular stimulation.

6. To study the role oscillations might play in the integration of cortical responses to stimuli covering multiple receptive fields, we studied the activity of 89 oscillatory cortical cells stimulated by large drifting gratings (coherent stimuli) and flashed bar sequences (incoherent stimuli). The data from these studies suggest that oscillations are not preferentially associated with coherent visual stimuli. Thirty-six of these cells oscillated only with incoherent stimulation, whereas 22 cells oscillated only with coherent stimulation. For the remaining 31 cells, oscillations typically occurred at higher frequencies for incoherent stimulation than for coherent stimulation.

7. Low-contrast drifting gratings were presented to 66 cortical cells to examine whether oscillations are present at very low response levels. Of these cells, 26 displayed some oscillatory activity. For none of these oscillatory cells did the strength of oscillation show any consistent relationship with contrast. When the oscillations observed in low-contrast responses are grouped together, we find that the strength of oscillations is inversely related to the mean firing rate.

8. The study of 59 cells in the LGN revealed the presence of oscillatory discharge in 31 cells. Of these cells, 10 exhibited oscillations that were an order of magnitude stronger than those found in the cortex. These strong geniculate oscillations, which are all ~ 50 Hz in frequency, are clearly independent of visual stimulation: the strength of oscillation was actually stronger when no visual pattern was presented. In contrast to oscillatory cortical cells, these LGN cells exhibited little variation in either oscillation strength or frequency between successive trials.

9. The data are consistent with a model in which oscillations seen in the visual cortex arise from spontaneous oscillations of a subpopulation of retinal ganglion cells. Because the physiological characteristics of oscillatory LGN cells are similar to those of some retinal ganglion cells, strong LGN oscillations in the 50-Hz range are likely to originate in the retina. The stimulus independence of both cortical and LGN oscillations is consistent with the proposal that such oscillations reflect spontaneous activity. Simulations based on measured firing properties of retinal ganglion cells and certain assumptions regarding geniculocortical connectivity suggest that the observed nature of cortical oscillations in the 50-Hz frequency range can be largely accounted for by the propagation of spontaneous activity through the central visual pathway.

10. The finding of strong and persistent LGN oscillations calls into question the exclusive association of cortical oscillations with intracortical mechanisms. Additionally, the instability and stimulus independence of oscillations support the notion that the oscillatory activity of single cortical neurons does not reflect parameters of patterned visual stimulation and may be an epiphenomenon of no obvious functional significance to the visual system.

INTRODUCTION

Rhythmic patterns of activity among neural populations are thought to play a fundamental role in the behaviors of various invertebrate organisms (see Jacklet 1989 for a review). Rhythms in the electroencephalogram (EEG) of the vertebrate cortex reflect the activity of a large population of neurons and are associated with states of alertness (Delagrange et al. 1989) and pathological conditions such as epilepsy (Dichter and Ayala 1987). However, the functional significance of many EEG patterns is still unclear (Freeman and Skarda 1985). Recent studies involving both local field potential and single-unit recordings within the visual cortex have revealed that oscillatory discharge in the 30- to 60-Hz frequency range occurs among populations of cortical neurons (Gray and Singer 1989; Gray et al. 1990). Because single-unit discharge in the central visual pathway underlies visual perception (Barlow 1972), these findings bring up the possibility that oscillations in the visual cortex may be of functional significance in the perceptual process.

Previous studies have suggested that the synchronized oscillations over populations of cortical neurons might result from intracortical networks that link common visual features between receptive fields (Eckhorn et al. 1988; Engel et al. In press; Grossberg and Somers 1991). On a more speculative note, these studies have hypothesized that oscillations emerge from interneural connections within the cortex and serve to encode visual stimuli. This proposition is based primarily on three findings: *1*) cortical oscillations are stimulus dependent; *2*) oscillations are synchronized over large distances and between cortical hemispheres (Engel et al. 1991a,b); and *3*) oscillations are not present in the lateral geniculate nucleus (LGN).

However, a mechanism for the generation of oscillations has not been identified (Gray et al. 1992b). Furthermore, methodological limits have prevented the establishment of an explicit relationship between stimulus attributes and oscillation strength and frequency (Gray and Singer 1989; Gray et al. 1990). The strength of a specific frequency of oscillation, relative to the noise present within a spike train, could not be measured by the previous analyses. This made it impossible to study stimulus dependencies in a quantitative manner. Furthermore, previous stimulus dependence results were based on limited sample sizes. Although oscillations were reported to be present in the kitten (Gray and Singer 1989), no comparisons were made between oscillations in adult and kitten cortex. Finally, there is a controversy concerning the presence of oscillatory discharge in the LGN. Several previous studies indicate their presence (Arnett 1975; Bishop et al. 1964; Munemori et al. 1984), but, in more recent work, it is reported that oscillations are specifically absent in the LGN (Gray and Singer 1989).

To more clearly elucidate the functional role of cortical oscillations, we systematically analyzed the nature of oscillatory discharge in a large number of physiologically classified cells within the LGN and the visual cortex of the cat and the kitten. Oscillations were quantified with respect to strength and frequency for responses to a variety of computer-controlled visual stimuli. For all cells, this analysis was done over a variety of temporal periods to study the stability and coherence of oscillations. Finally, the receptive-field properties and laminar locations of cells that exhibited oscillations were tabulated to determine the distribution of cells that exhibit oscillatory discharge.

Our results show that cortical oscillations are highly unstable and do not exhibit consistent dependencies on the properties of visual stimulation. Oscillations are present among both simple and complex cells within all layers of the cortex in both kittens and adult cats. Our findings also suggest that oscillatory discharge does not arise exclusively from intracortical interactions. The strength of oscillations in LGN spontaneous discharge and the presence of oscillations within the input layers of the visual cortex implicate a precortical origin. This origin is also suggested by numerous reports of spontaneous rhythmic activity in the retina (Ariel et al. 1983; Barlow et al. 1964; Kuffler 1953; Robson and Troy 1987), optic nerve (Laufer and Verzeano 1967), and LGN (Arnett 1975). In contrast to recent suggestions that these oscillations encode visual information (Engel et al. In press, Singer 1990b), the data here suggest that oscillatory single-unit discharge in the visual cortex may play no clear functional role and originates primarily from precortical spontaneous activity.

METHODS

Physiological preparation

Twenty-eight adult cats (1.9–4.6 kg) and 12 kittens at postnatal *day 28* (350–580 g) were studied by standard extracellular recording techniques. Acepromazine (0.5 mg/kg) and atropine (0.3 mg for adults, 0.05 mg for kittens) were injected subcutaneously 30 min before surgery for tranquilization and reduction of secretion. During halothane-induced anesthesia, catheters were placed in the femoral veins of each forepaw, and an endotracheal tube was secured. Needle electrodes were positioned in fore- and hindlimb muscle to monitor the electrocardiogram. A thermistor was inserted rectally to monitor core body temperature. After the animal's head was secured in a stereotaxic holder via ear bars, a craniotomy was performed over the area 17 representation of area centralis close to the sagittal midline, and the dura was reflected. For adults, this region is located at P4,L3, and for kittens, it is located just anterior to the lambda suture. Four of the adult cats were used for LGN recordings. In these animals the craniotomy was performed at stereotaxic coordinates A6,L9.

Animals were paralyzed with a loading dose of gallamine triethiodide (Flaxedil) and artificially respirated with a mixture of 75% N_2O-25% O_2. Two Levick-type tungsten-in-glass electrodes, encased in a common tube driven by a micropositioner, were positioned over the exposed cortex, and the area was sealed by agar covered with wax. The interelectrode distance within the common tube was ~500 μm. Throughout the experiment N_2O was supplemented by a continuous infusion of thiamylal sodium (Surital) at 1 $mg \cdot kg^{-1} \cdot h^{-1}$. Paralysis was maintained by continuous infusion of Flaxedil (10 $mg \cdot kg^{-1} \cdot h^{-1}$) mixed with dextrose-supplemented Ringer. Electrocardiogram and EEG data were monitored to help assess the level of anesthesia. Expired CO_2 was maintained at ~4.25% by occasional adjustments of the stroke volume of the respiration pump. Body temperature was automatically maintained near 38°C by a feedback controlled heating pad and lamp.

Before electrophysiological recordings, the pupils were dilated with atropine sulfate (0.5%), and the nictitating membranes were retracted by topical phenylephrine hydrochloride (10%). Corneas were protected with contact lenses with artificial pupils of 4 mm diam. Optic disk position was rear projected onto a tangent screen ophthalmoscopically for each eye. Eyes and contact lenses were cleaned every 8 h during the experiment.

Histology

For each electrode penetration, two or three electrolytic lesions were made at regular intervals (between 500 and 1,000 μm) along each electrode track as the electrodes were withdrawn from the cortex. This was done by passing DC current through the electrode (5 mA for 5 s). At the end of each experiment, the animal was given an overdose of pentobarbital sodium (Nembutal) and perfused through the heart with buffered saline (0.9%) followed by Formalin (10%). Blocks of visual cortex were cut in the plane of the electrode tracks, and 40-μm frozen sections were cut and stained with thionin. Lesions were located, and electrode tracks were reconstructed to determine positions of recorded cells. The cortical neurons studied were all located in area 17, and all cortical lamina were represented in the sample, although the majority of cells was in layers 4 and 6. The majority of LGN cells was recorded in layers A and A1.

Recording procedures

Action potentials from individual cells were isolated by amplitude-based discrimination after appropriate amplification and filtering. The occurrence of each action potential was recorded by a computer with a temporal resolution of 1 ms and, in some cases, 0.1 ms.

Bar stimuli back projected on a tangent screen 57 cm from the cat's eyes were manually drifted during electrode advancement to isolate and initially characterize single-unit activity. A half-silvered beam splitter placed in front of the cat allowed for visual stimulation either by targets projected onto the tangent screen or by stimuli produced on two cathode ray tube (CRT) displays (48 cd/m^2). The displays were positioned so that they could be used to independently stimulate each eye from a distance of 57 cm. After isolation of a neuron on the basis of action-potential amplitude, a manually controlled search program was used in conjunction with these displays to estimate ocular dominance, orientation and spatial frequency selectivity, and receptive-field type.

For 342 cortical cells the orientation, direction, and spatial frequency of sinusoidal gratings at 50% contrast and drifting at a temporal frequency of 2 Hz were then varied in randomly interleaved sequences to determine exactly the receptive-field type and optimal sensitivities. During these runs, peristimulus time histograms (PSTHs) and interspike interval histograms were accumulated. For each CRT, mean luminance was maintained in the intervals when no grating was present (2–3 s). Except for cells that exhibited length tuning, large gratings ranging from 8 to 20° diam and centered on the receptive field were used. Receptive fields were classified as simple or complex by computing the degree of 2-Hz modulation in the PSTHs. A cell whose 2-Hz response harmonic was greater than its mean firing rate was classified as simple; otherwise, the cell was classified as complex. Complex cells with very little length summation and large receptive fields were classified as special-complex. The sync pulses corresponding to the temporal frequency of the gratings were recorded by computer with the same temporal resolution as the action potentials.

The 59 geniculate cells were classified into X and Y groups according to the linearity of their spatial summation. Spatial frequency selectivity was initially measured with the use of 50% contrast sinusoidal gratings that were temporally modulated by counterphase at a frequency of 2 Hz. The linearity was tested by varying the spatial phase of such gratings (null test). Cells showing a null response rate at a particular spatial phase were classified as X-cells (Enroth-Cugell and Robson 1966).

Visual stimulation

Analysis was carried out for 342 cells with discharge rates to optimal stimulation >5 spikes/s. After receptive-field classification, two types of stimuli were used to study the potential stimulus dependence of oscillatory discharge. For the 188 binocular cells studied, drifting gratings of optimal spatial frequency and orientation were presented dichoptically. For 268 cells, small bars of appropriate orientation and size were flashed to invoke neural discharge.

For the binocular studies the spatial phase between the gratings presented to the two eyes was varied in a randomly interleaved manner. This allowed a determination of the degree of linear summation between the receptive fields of the two eyes. A null condition, consisting of mean luminance unpatterned stimulation to both eyes, and monoptic stimulation conditions were interleaved among the dichoptic stimuli. Each stimulus condition consisted of a 4-s presentation, which was typically repeated four times in a semirandom sequence. For oscillation analysis, responses from interleaved monocular and binocular conditions were usually compared. When dichoptic and monoptic presentations are interleaved, monocular response rates are generally reduced (Ohzawa and Freeman 1986). Presumably, this is due to adaptation. For cases in which the response rate of the interleaved monocular conditions was <5 spikes/s, we compared the binocular discharges with monocular responses obtained from monoptic orientation and spatial frequency runs.

In the reverse correlation technique (Jones and Palmer 1987), a random sequence of flashed bright and dark bars of appropriate orientation and size, presented at an array of positions centered on the receptive field, is used to activate neural discharge. The duration of each bar presentation was either 52 or 39 ms, and only one bar was present at any point in time. Bar size was set to the smallest dimensions that elicited neural discharge. Bar widths were ≤0.5°, and bar lengths were between 1 and 10°. Each trial consisted of a different random sequence in which bars brighter or darker than the mean luminance background were presented once at every possible position within the array, which usually spanned a visual area of 6 by 6°. Trials were presented successively up to 60 times. Because of the randomness of each of these trials, the stimulus is both spatially and temporally incoherent. The lack of any consistent pattern or motion within the trials makes this stimulus perceptually noiselike. By contrast, the drifting sinusoidal grating extending throughout and beyond the receptive field presents input that is spatially and temporally coherent within the limit of receptive-field spatiotemporal filtering. Because the reverse correlation method can accurately map receptive-field structure by inferring the particular causal stimulus associated with each spike, receptive-field classifications provided by the initial grating stimulation were confirmed. All cortical cells with large first harmonic components in their PSTHs to drifting gratings had nonoverlapping ON and OFF regions revealed by this technique and were thus confirmed to be simple cells.

Data analysis

Detailed autocorrelation analysis was performed after data acquisition to examine common firing intervals. The distribution of these intervals into bins representing different interspike intervals is called the autocorrelogram, as illustrated in Fig. 1. The height of each bin represents the number of spike pairs observed that are separated by the interval represented by the bin. Rhythmic discharge will produce a regular pattern of peaks in the autocorrelogram whose spacing corresponds to frequency. To ensure that peaks in the correlogram are not simply due to periodicities in the stimulus, autocorrelograms are computed for shuffled spike trains (Perkel et al. 1967). Periodicities in the shuffled correlograms are based solely on the stimulus. To examine rhythmic discharge of a neural origin, the shuffled correlogram is subtracted from the raw correlogram.

The importance of ascertaining whether periodicities in the spike train are of neural or stimulus origin can be seen by examin-

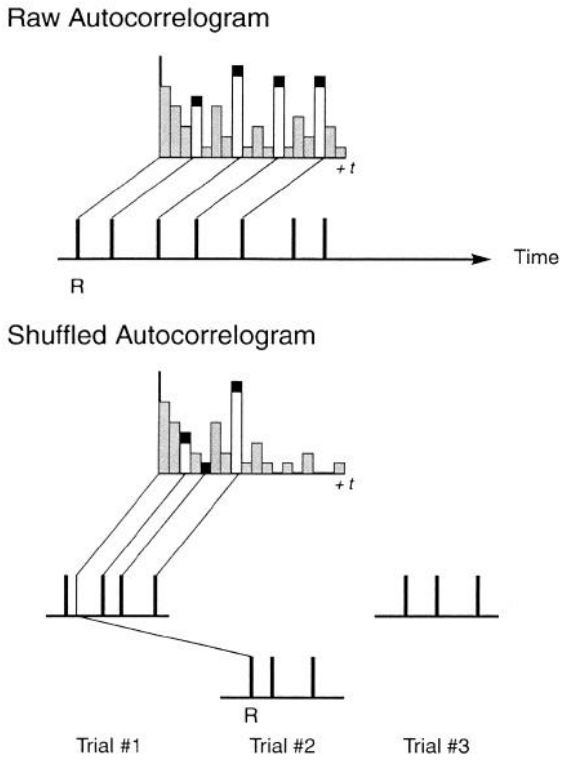

FIG. 1. Raw autocorrelogram shows distribution of intervals between action potentials in the spike train. The autocorrelation distribution is computed by taking a reference spike, here labeled R, and searching forward in the spike train for subsequent spikes. Spike intervals up to the limit of $+t$ are tallied in the correlogram. Unfilled bins are incremented (■) according to this portion of the spike sequence. The process is then repeated by moving the reference R to successive spikes. Periodicity in the autocorrelogram is indicative of rhythmic discharge in the spike train. For the autocorrelograms shown in subsequent figures, $t = 256$ ms. The shuffled autocorrelogram is used to compute periodicities in the spike train that are associated with periodicities in the visual stimulus itself. This correlogram is computed by applying the autocorrelation method to 2 spike trains resulting from different repetitions of the same stimulus. In this example, reference spikes are taken from trial #2, and the incrementing spikes are taken from trial #1 of the same stimulus. This shuffling between different trials is repeated with the use of different trial pairs to construct a shuffled correlogram.

ing the autocorrelograms from the two LGN cells shown in Fig. 2. Both of the *top two autocorrelograms* were obtained from analyzing single-unit recordings within the LGN, and both display a very regular discharge. For the cell on the *left*, the shuffled correlogram indicates strong periodicity at the frequency of the refresh rate of the CRTs used for visual stimulation (76 Hz). By contrast, the shuffled correlogram on the *right* shows no periodicity. We can therefore conclude that the oscillations for the cell on the *left* are related to the stimulus, whereas the oscillations observed on the *right* are independent of periodicities in the stimulus. This conclusion is reenforced by looking at the difference between raw and shuffle correlograms, which are displayed in the *bottom row*. For the cell on the *left*, virtually all periodicities are eliminated after shuffle subtraction, whereas for the cell on the *right*, the periodicities remain. For the cell on the *left*, no periodicity is visible in the shuffle-corrected correlogram. Because many LGN cells are sensitive to high temporal frequencies, LGN cells often discharge in synchrony with the screen refresh. Although cortical cells typically do not respond to gratings of temporal frequencies higher than 15 Hz, some cells, when responding to 2-Hz gratings, show discharge modulation at the CRT flicker frequency. Because of these stimulus-related periodicities, all measurements of oscillatory discharge were made with the use of shuffle-subtracted autocorrelograms, and therefore they reflect neurally generated oscillations.

Some discharge records showed modulation at the flicker frequency even after shuffle subtraction. For such cells there are two possibilities: *1*) that neurally originating oscillations are actually occurring at the same frequency as the stimulus, or *2*) that the shuffle process is not always an adequate control for stimulus-related periodicities. The second possibility could be explained by a nonlinear addition of neural connectivity and stimulus effects (Melssen and Epping 1987). Because of this possibility, cells showing oscillatory behavior at 76 Hz in both the shuffle and shuffle-subtracted autocorrelograms were classified as nonoscillatory. It is therefore possible that the current sample underestimates the incidence of oscillatory discharge around 76 Hz. Oscillatory activity around 76 Hz is unlikely to be prevalent, however, given that only 3% of all oscillations observed were at frequencies >63 Hz.

RESULTS

Quantification of oscillations

To examine the frequencies present in the discharge of a cell, an autocorrelation function spanning spike intervals up to 256 ms was constructed. Computation of the discrete Fourier transform of this function yields an analog to the power spectrum of a continuous signal with a frequency resolution of 2.8 Hz for an autocorrelogram temporal resolution of 1 ms. Two factors constrain the power spectra that are generated by this method. The first is the Nyquist limit, which relates the maximum frequency that can be calculated by a Fourier transform to the sampling rate. Because autocorrelogram bins are 1 ms in width, the Nyquist frequency for such data is 500 Hz. A second limitation is the nonlinearity of the binning process in which interspike intervals are assigned to bins of 1 ms in width (no smoothing

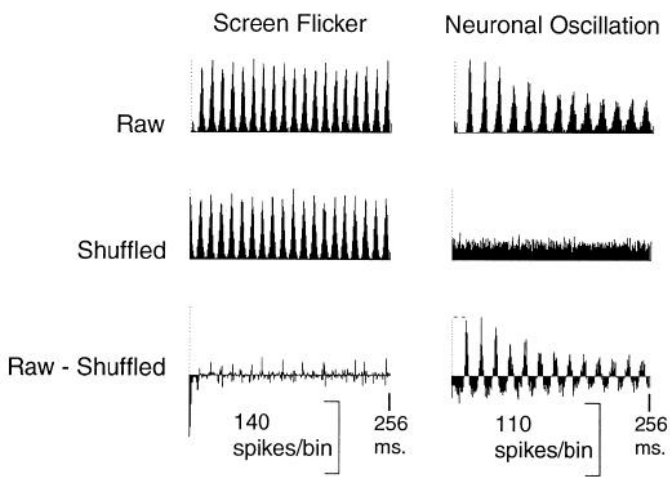

FIG. 2. Raw correlograms from 2 lateral geniculate nucleus cells are shown in the *top row*; both are indicative of rhythmic discharge. For the cell on the *left*, there is a clear periodicity in the shuffled correlogram, which, because of the shuffle method, can only be due to a periodicity within the visual stimulus itself. In this case the shuffle periodicity occurs at a frequency of 76 Hz, which corresponds to the screen refresh rate of the cathode ray tube monitors used for visual stimulation. For the cell on the *right*, no periodicities are evident in the shuffled autocorrelogram, indicating that the cell's rhythmicity is not due to the stimulus. By subtracting the shuffled from the raw correlogram, we obtain a difference correlogram that indicates the degree to which discharge periodicities are of neural origin.

was performed on autocorrelograms). This introduces the possibility that the peaks seen below 500 Hz actually reflect the aliasing of signals between 500 and 1,000 Hz in the spike train (Schild and Schultens 1986). This possibility was examined by computing the power spectra for strongly oscillatory cells that were recorded with a temporal resolution of 0.1 ms. For five cells examined in this way, the Nyquist frequency was 5,000 Hz, and the 500- to 1,000-Hz frequency range could be explicitly examined. None of these cells showed any distinguishable peaks in the 500- to 1,000-Hz frequency range.

Oscillation frequency and strength were quantified by searching for discernable peaks in the 29- to 78-Hz frequency range of the power spectrum. This frequency range was examined because, in previous studies, oscillations were found in this range by a different method of analysis (Gray and Singer 1989) and because it is the frequency range of EEG rhythms of potential sensory significance in the olfactory bulb (Freeman and Skarda 1985) and visual cortex (Freeman and van Dijk 1987). In our analyses, oscillation frequency was identified as the frequency having the highest amplitude within this range of the power spectrum. Peak height was averaged over a frequency window 9.5 Hz in width that was centered on the optimal frequency. Noise was estimated by averaging the power between 250 and 500 Hz, with the use of the assumption that no signal was present in this frequency range. This assumption is corroborated by the absence of any discernable peaks in the upper 250 Hz of the power spectra. Additionally, for the cells that could be analyzed up to 5,000 Hz, power spectra were always flat beyond 250 Hz. On the assumption that the noise is flat across all frequencies, a signal-to-noise (S/N) ratio was computed with the use of the averaged peak height and the high-frequency noise estimate (Press et al. 1988). A neural discharge record was classed as oscillatory if three criteria were met: *1*) the power at frequencies near the optimal was larger than the noise estimate; *2*) the S/N ratio exceeded 1.5; and *3*) the peak was not at the screen refresh frequency of 76 Hz.

With the use of these criteria, all cells can be classed as either oscillatory or nonoscillatory given a sufficient number of spikes. For cells whose discharge shows regular activity in the autocorrelogram, a sharp peak is present in the power spectrum at the frequency corresponding to the inverse of the predominant interspike interval, as shown in Fig. 3*B*. By contrast, discharges with smooth autocorrelograms result in power spectra with no discernable peaks beyond 0 Hz (Fig. 3*A*). Many cells do not fall into these extremes: their autocorrelograms might contain several peaks at varying intervals. For these neural discharge records, it is particularly important to quantify the strength of specific frequencies relative to the noise present. Previous analyses of oscillations have been made by fitting a damped sine wave to autocorrelograms and setting a goodness-of-fit criterion to the first two peaks in the autocorrelogram (Gray and Singer 1989) or by measuring the modulation within the first peak and trough of a smoothed autocorrelogram (Gray et al. 1990). This method emphasizes the most common interspike interval, but it ignores the higher order autocorrelations that a multicycle oscillation will produce. Because of this, the fitted sinusoid's amplitude does not accurately quantify the *strength* of an oscillation frequency within the spike train. This is an important consideration if one wishes to compare oscillations between different groups of cells or under different stimulus conditions. In particular, the relative strength of a given frequency cannot be evaluated when multiple frequencies are present. For example, an autocorrelogram showing many peaks at different spacings can have two primary peaks that can be fitted quite well to a damped sinusoid, as illustrated in Fig. 4. However, if all frequencies up to 500 Hz are examined by the power spectrum method, we find that the predominant frequency is not distinguishable from other frequencies. Conversely, the discharge records of cells with low firing rates can yield autocorrelograms not well fit by a sine wave, but that, when analyzed by the power spectrum method, reveal strong single frequency components.

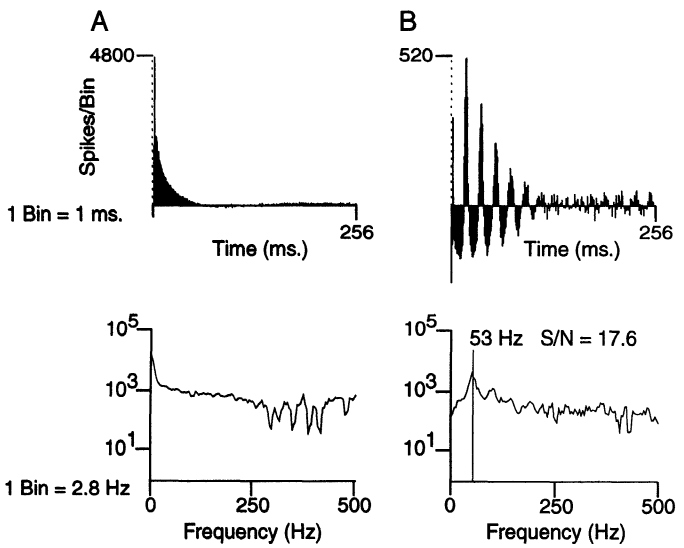

FIG. 3. Autocorrelograms and power spectra corresponding to a nonoscillatory complex cell (*A*) and a strongly oscillatory lateral geniculate nucleus cell (*B*) are shown here. Periodicities are quantified with the use of the power spectra (*bottom row*) of spike trains, which are computed by taking the discrete Fourier transform of the discharge autocorrelograms in the *top row*. Autocorrelograms are reflected to span intervals from −256 to +256 ms before the Fourier transform. These spectra, plotted here on a log-linear scale, show the distribution of frequencies present in the spike trains. The high-frequency tail (from 250 to 500 Hz) is used to estimate the noise in the spike train. For the cell in *A*, a smooth autocorrelogram based on 25,787 spikes accumulated during reverse correlation stimulation yields a power spectrum whose sole peak is at 0 Hz. This indicates that the 0-Hz frequency is dominant in the spike train. By contrast, the cell shown in *B* exhibits very rhythmic discharge. The power spectrum of this discharge (which contains 3,800 spikes) shows a distinguishable peak at 53 Hz, which has a magnitude 17.6 times larger than that of the noise.

Stability

The stability of oscillatory discharge was analyzed by comparing the power spectra of spike trains associated with different trials of the same stimulus. For cells whose accumulated autocorrelograms showed oscillations in response to sinusoidal gratings, each 4-s trial was analyzed individually. For cells studied with the reverse-correlation stimulus, autocorrelograms were accumulated over three experimental time scales: the entire experiment (from 20 to 80 trials); groups of five consecutive trials; and, if the firing was rela-

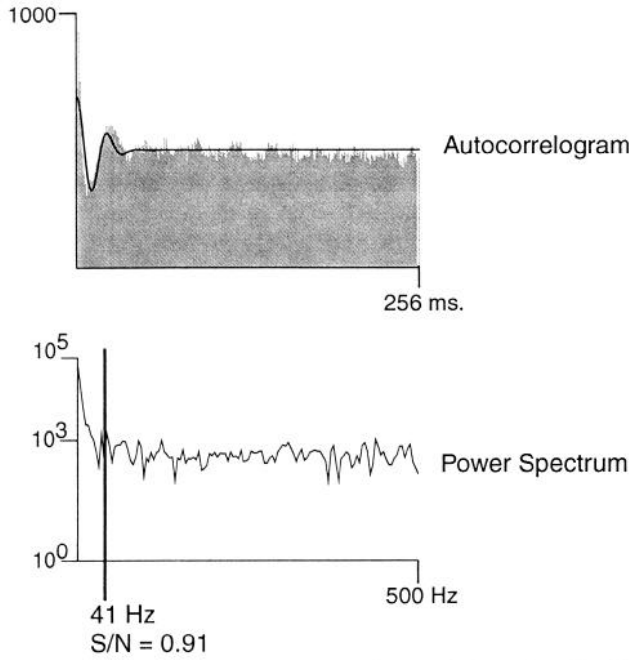

FIG. 4. In this example, a raw autocorrelogram is shown (gray), which, on initial examination, would seem to indicate periodic discharge. This perception would be confirmed by fitting a damped sine wave (black) to the 1st few peaks. However, the fit of the sine wave is particularly poor at intervals larger than ~70 ms. Thus the fitted sine wave is unable to quantify the level of high-frequency noise in the complete autocorrelogram. By contrast, the power spectrum displays the relative strength of all frequencies up to 500 Hz and reveals that many frequency components are present in the spike train, none of which is dominant. If we examine the spectrum at the frequency of the fitted sinusoid (41 Hz), we obtain a signal which is not very distinguishable from noise (as measured by the average power from 250 to 500 Hz).

tively vigorous (>100 spikes/trial), individual trials. For each period examined, a peak frequency and S/N ratio were computed independently from the other periods. This allowed study of the changes in both the frequency and strength of oscillations over time.

All cortical oscillatory discharge examined in this manner was highly variable in frequency and strength. For some cells, there were dramatic changes in oscillatory frequency between successive trials, as is seen in Fig. 5, *B–D*. In other cases, oscillations were only apparent on certain trials (Fig. 5, *F* and *H*) and were not apparent when all the trials were averaged together (*E*). These observations are in agreement with previous studies of cortical oscillatory discharge, all of which have pointed to its highly transitory nature (Eckhorn et al. 1989; Gray et al. 1992a). The lack of oscillations within shuffled autocorrelograms demonstrates that oscillations are not locked to stimulus onset. This is also in agreement with prior observations.

Only one temporally consistent pattern of intertrial changes was observed. For several cells the strength of oscillatory discharge showed strong adaptation on the order of seconds. For these cells, oscillations were only observable during the first few 4-s trials of an experimental run, as illustrated in Fig. 6. The beginning of a run is the only luminance transient during the course of the experiment because, during the run, mean luminance was maintained in the intertrial intervals. Oscillatory adaptation could therefore be related to the initial step change in luminance. The possibility also exists, however, that the intertrial interval, which was between 2 and 3 s, was not of sufficient length to allow recovery from contrast adaptation (Ohzawa et al. 1985). Because changes in both luminance and contrast were present at the beginning of the experiments, we cannot assess which factor is responsible for the adaptation. However, the time course of this adaptation matches that seen in the adaptation of oscillatory optic tract potentials to luminance changes (Laufer and Verzeano 1967).

The transitory nature of oscillatory discharge complicates comparisons between stimulation conditions and physiological cell types, because it implies that no cortical cell produces consistent oscillations in response to visual stimulation. This is in contrast to the metric of mean firing rate, which is relatively consistent on a trial-to-trial basis for most cortical cells. For the data presented here, the time period that contains the strongest oscillations, as measured by S/N ratio, is said to characterize that cell's potential to oscillate in response to a stimulus. The transitory nature of

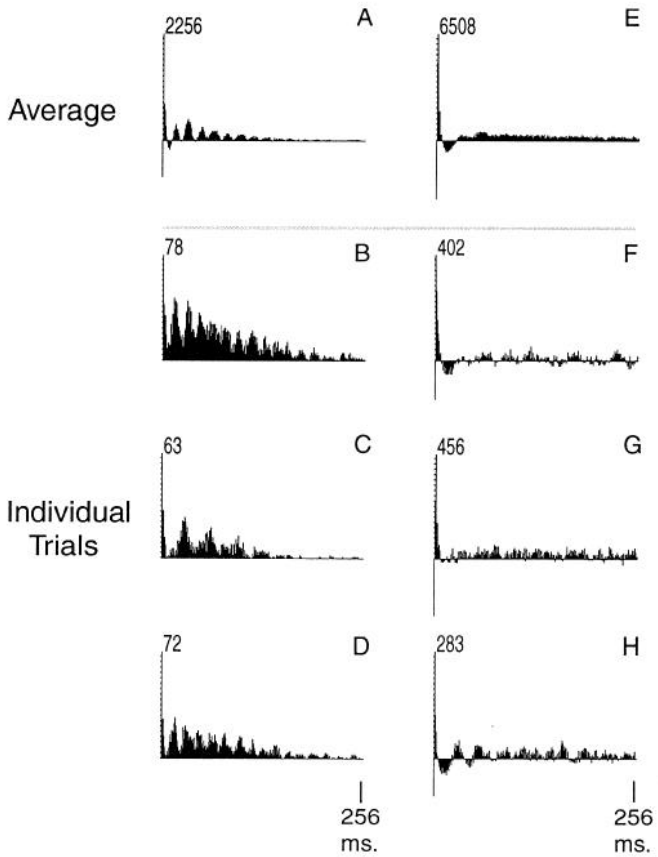

FIG. 5. Two examples of the instability of oscillatory discharge in the cortex are shown here. Numbers at the top of each correlogram indicate the scale (spikes/bin) for that correlogram. The average correlograms are computed over all repetitions. For the cell on the *left* (*A–D*), the average discharge over 50 repetitions has a periodicity at 40 Hz (*A*). Individual trials, which are computed from 4 s of visual stimulation, show dramatic variations in the frequency of discharge. In the 1st individual trial of the response, shown in *A*, the cell oscillates at 60 Hz (*B*). Several trials later, the cell oscillates at 30 Hz (*C*). The cell then reverts back to 60 Hz (*D*). For the cell on the *right* (*E–H*), the average over 80 repetitions shows no significant periodicity (*E*). Yet some individual trials, (*F* and *H*) do show oscillations.

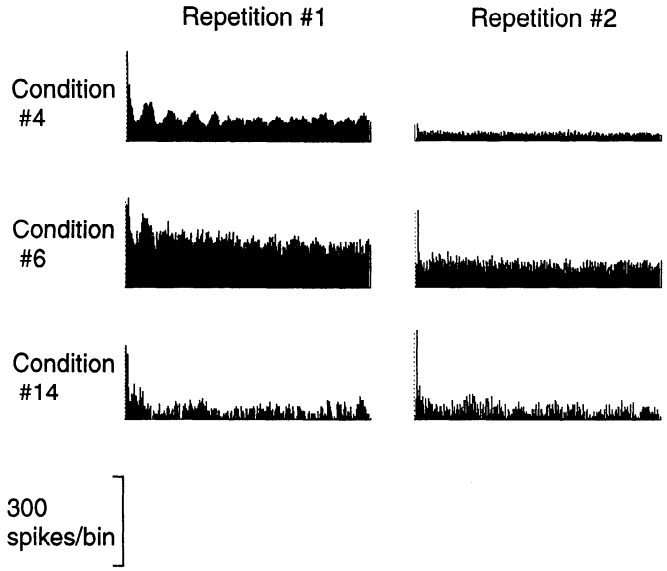

FIG. 6. Oscillations can exhibit rapid adaptation. Responses to the 1st 3 stimuli are shown in the *left column*. In this example these presentations correspond to conditions 4, 6, and 14 of an experiment in which the interocular phase between drifting gratings was varied. In this example the initial runs shown in the *left column* exhibit oscillations, whereas the following repetitions of the same stimuli do not. For this experiment, oscillations never reappeared after the initial adaptation.

oscillations makes this characterization difficult to substantiate conclusively. For example, strong oscillations in response to a single trial of monocular stimulation might be seen in a cell that displays weak, but consistent, oscillations under binocular stimulation. Given a long enough recording, however, that same cell might exhibit a brief period of strong oscillations at a different frequency under binocular stimulation. This intrinsic variability necessitates the use of large sample sizes and recording times to demonstrate any categorical differences. The lack of long-term stability also makes it important to measure the strength of putative oscillation frequencies relative to the noise present in the spike train.

Development

There are several reasons to expect that the nature of oscillatory discharge might change during postnatal development. Oscillatory discharge involves firing at regular intervals that might be less likely for cells of the kitten cortex, given the increased variability of neural discharge and the relative sluggishness of cortical responses (Hubel and Wiesel 1963). If oscillations are dependent on synaptic networks, the immaturity of afferent (Tsumoto and Suda 1982) and intracortical connections might preclude oscillations. On the other hand, if oscillations provide an important signal for activity-dependent reorganization (Singer 1990a), then oscillations might be especially prevalent or strong at early stages of development.

To discriminate between these possibilities, we have compared the oscillatory discharge in kittens at 4 wk postnatal with that of adults. Reliable single-unit recording may be obtained from kittens at 4 wk postnatal, but the visual cortex is highly susceptible to the nature of visual input (Olson and Freeman 1980). Therefore developmental processes must be very active at this postnatal age. In the kitten, oscillatory discharge was observed for 8 of 40 simple cells and for 19 of 40 complex cells. To study developmental differences in oscillatory discharge, the oscillations from these 27 cells were compared with the oscillations from 115 oscillatory cortical cells in the adult. As shown in Fig. 7, oscillations in kitten cortex are most predominant at the lowest frequencies studied: 40% of the oscillations are at frequencies between 28 and 32 Hz. When the frequency distributions are grouped with 5 degrees of freedom, χ^2 analysis reveals a significant difference between adult and kitten oscillatory discharge frequency ($\chi^2 = 43$, $P \ll 0.001$). This difference is due primarily to the greater incidence of oscillations between 36 and 44 Hz in the adult ($\chi^2 = 29$). Thus, although the incidence of oscillatory cells does not change during development, the distribution of oscillatory frequencies is different between the kitten and the adult cat.

Stimulus dependence

BINOCULARITY Comparisons were made of binocular versus monocular responses accumulated over the same period of time. In contrast to a previous report of enhanced oscillations using binocular, as compared with monocular, stimuli (Gray et al. 1990), we find no systematic difference. In fact, for many cases, the opposite is true, as illustrated in Fig. 8. For the cell shown in Fig. 8, despite the reduced firing rate for monocular stimulation, the strength of monocular oscillation is stronger than that seen in the binocular case. For 98 cells that displayed oscillations in the binocular protocol, we find that the majority oscillate under both monocular and binocular stimulation, as summarized in Fig. 9. The number of cells that oscillate solely under monocular stimulation is approximately equal to the number that only oscillate under binocular stimulation. For cells whose binocular and monocular oscillations were within 4 Hz of each other in frequency ($n = 44$), a comparison was made between S/N ratios, as shown in the *right* of Fig. 9. Around one-half of these cells exhibited stronger oscillations binocularly than monocularly. The remainder of the cells exhibited oscillations that were either approximately equal in strength (S/N ratios that differed <13%) or, as shown in Fig. 8, stronger under monocular stimulation.

For cells that oscillated under binocular conditions, the dependence of these oscillations on the phase difference

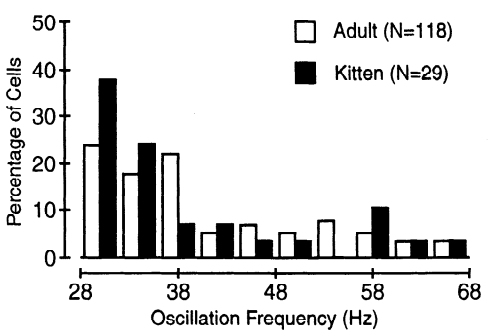

FIG. 7. Distribution of oscillation frequencies differs between adult and kitten cortical cells. Each bin represents a 4-Hz range of frequencies. The major difference in the distribution is ~36 Hz, at which very few kitten cells exhibit oscillatory activity. Note also the predominance of low-frequency (28–32 Hz) oscillators in the kitten.

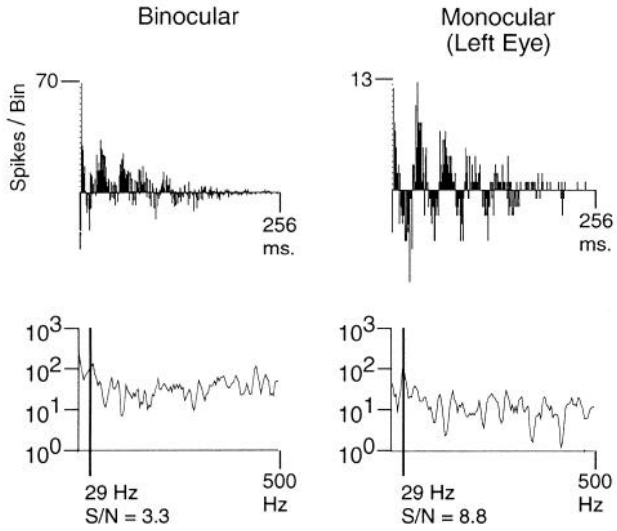

FIG. 8. In this example a comparison is made of oscillations that occurred during monocular compared with binocular stimulation. Binocular stimulation was accomplished by presentation of drifting sinusoidal gratings to the 2 eyes. *Left autocorrelation* is from a simple cell's response to such stimulation. The cell oscillates at 29 Hz to gratings whose phase difference was adjusted to yield maximal firing. The same cell oscillates at 29 Hz in response to stimulation in the left eye only. Because the absolute number of spikes is much higher for binocular as compared with monocular activation, scales for the autocorrelograms, shown at the *bottom*, are substantially different. However, the oscillation is stronger for monocular stimulation, as can be seen by the large signal-to-noise ratio of the monocular response power spectra. This can be visually verified by the sharpness of the peaks in the autocorrelogram on the *right*. Thus, even though the firing rate is lower with monocular stimulation, as can be seen by the different scales of the 2 autocorrelograms, oscillations are stronger.

between the gratings presented to the two eyes was examined. In agreement with previous studies, all binocular simple cells and ~40% of binocular complex cells show a periodic modulation of response rate with interocular phase (Ohzawa and Freeman 1986). Oscillation strength for these cells is independent of this modulation. For any cell, the strongest oscillations were just as likely to occur for stimuli that elicited weaker or stronger response rates. For complex cells whose response rates were independent of interocular phase, the strength of oscillations was also independent.

As shown in Fig. 10, those cells that oscillated under both monocular and binocular stimulation exhibited no consistent trend between oscillation frequency and type of stimulation. Oscillation frequencies were classed as similar if they were within 4 Hz of each other. Such cells fall within the region bounded by the two diagonal lines of Fig. 10. The majority (n = 44) of cells oscillated at similar frequencies for binocular and monocular stimulation. For cells that oscillated at different frequencies, nearly equal numbers discharged at higher frequencies with monocular stimulation and with binocular stimulation (above and below the diagonal lines, respectively).

COHERENCE. To determine the relationship between oscillations and the coherence of visual stimuli presented, the responses to sinusoidal gratings and reverse correlation stimulation were compared for 89 oscillatory cortical cells. Because the reverse-correlation stimulus produces a much weaker response for each presentation than gratings, autocorrelograms were generally sparser in the former case. However, periodic discharge was seen by the power spectra method for the reverse-correlation responses of 63 cortical cells. An example of such discharge is shown on the *left* of Fig. 11. As shown in Table 1, the number of cells that oscillated only with incoherent stimuli is greater than the number that oscillated only with coherent stimuli. In contrast to the comparison of binocular and monocular responses, slightly less than one-half of the cells studied oscillate under

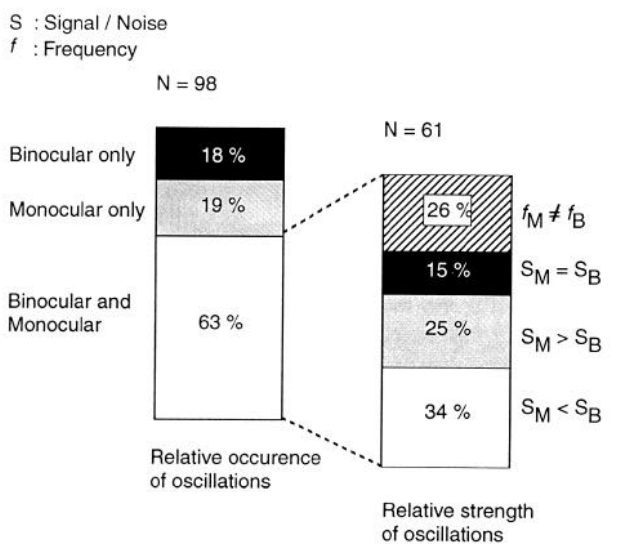

FIG. 9. Dependence of oscillatory discharge on the binocularity of visual stimulation is summarized here. Although the majority of cells oscillated to both monocular and binocular stimulation, 37% of the cells studied oscillated only with one or the only type of stimulation. Of the 61 remaining cells 40% showed monocular oscillations, which were equal to or stronger than those seen with binocular stimulation ($S_M \geq S_B$), such as in Fig. 8.

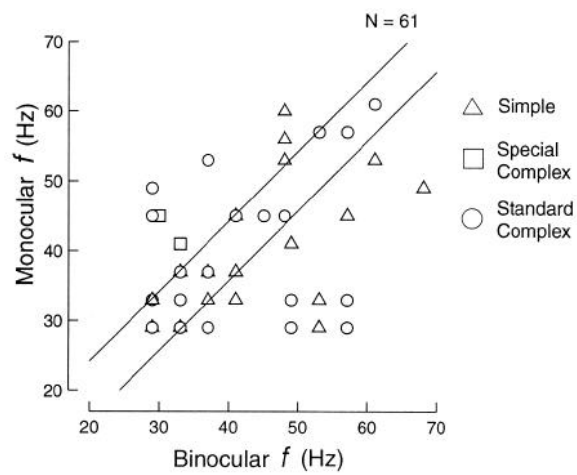

FIG. 10. For cells that oscillated under both binocular and monocular stimulation, the frequencies of the maximal oscillation under the 2 types of stimulation are shown here. Diagonal lines show the region of ±4 Hz within which oscillations were considered to be at the same frequency. Comparison of signal-to-noise ratios for binocular and monocular stimulation seen in Fig. 9 was made only for the 44 cells that fall within this diagonal region. The vast majority of cells that oscillate under both binocular and monocular stimulation oscillate at nearly the same frequency. The number of distinct points is less than the total number of points because the frequency resolution of the Fourier transform (2.8 Hz) results in overlapping data points.

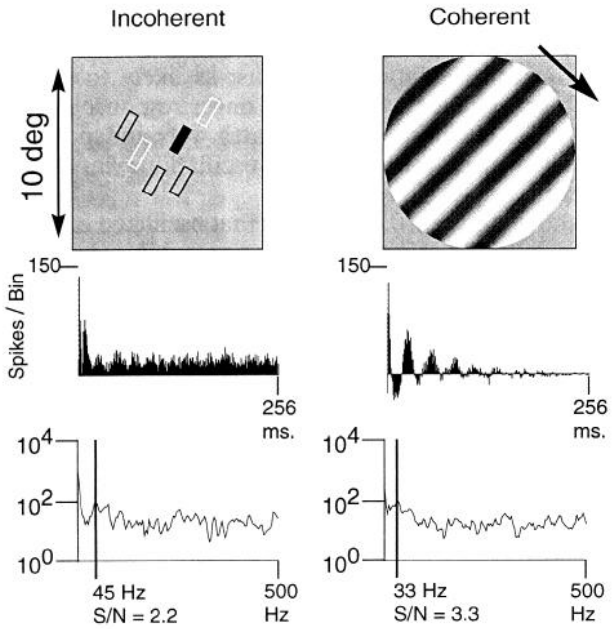

FIG. 11. As shown in these correlograms and power spectra from 2 different cells, oscillations can be observed with both incoherent and coherent stimulation. Incoherent stimulation is accomplished by the presentation of small bars of random position within the receptive field and of a luminance either brighter or darker than the background. In the stimulus depiction on the *left*, the short history of the stimulation immediately before the presentation of the solid dark bar is indicated by the outlined bars. All bars are of appropriate size and orientation so as to elicit neural responses. Coherent stimulation consists of smoothly drifting sinusoidal gratings that extend beyond the receptive field.

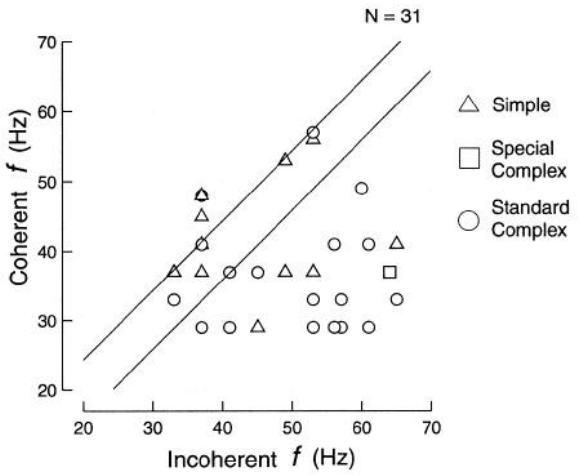

FIG. 12. For cells that oscillate under both coherent and incoherent stimulation, the frequencies of oscillation seldom correspond. With the use of the same criteria for frequency similarity as used for the summary of Fig. 10, we see that relatively few cells oscillate at the same frequency. Unlike Fig. 10, very few points fall within the diagonal region. In the majority of cases, oscillation frequency is higher for incoherent stimulation than for coherent stimulation, as indicated by cells located in the *bottom right*. Because of overlap, the number of distinct points is less than the total number of points.

both coherent and incoherent stimulation. Only around one-half of the cells that oscillate in response to one type of stimulus oscillate with the other type of stimulation.

The lack of any strong correlation between oscillations under coherent and incoherent stimulation suggests that oscillatory discharge among individual cells might depend on the frequency characteristics of visual stimulation. This possibility is supported by examination of the responses from the 31 cells that oscillated with both types of stimulation. As shown in Fig. 12, the frequencies of oscillation with coherent and incoherent stimulation are seldom within 4 Hz of each other. For these cells, 56% oscillate at higher frequencies with incoherent stimulation. The mean frequency of oscillations with incoherent stimuli is significantly higher than the mean seen for coherent stimulation ($t = 4.0$, $P < 0.001$). This tendency is also evident in the comparison of the population of oscillatory responses with coherent and incoherent stimulation. The mean frequency for incoherent stimulation is 47 Hz, which is significantly higher than the mean of 38 Hz seen among coherent stimulus oscillations ($t = 4.9$, $P \ll 0.001$). This difference is not seen with respect to oscillation strength: S/N ratios are similar for coherent and incoherent stimulation ($t = 1.9$). Thus the coherence of visual stimulation seems to affect the likely frequencies of oscillatory discharge, but not its incidence.

TABLE 1. *Oscillations in the respones to incoherent and coherent stimulation*

	Number of Cells	Frequency, Hz	Signal-to-Noise
Incoherent only	36	$f_i = 46.4 \pm 1.8$	$S_i = 2.9 \pm 0.4$
Coherent only	22	$f_c = 38.1 \pm 1.6$	$S_c = 3.5 \pm 0.3$
Incoherent and coherent	31	$f_i = 47.7 \pm 1.9$ $f_c = 38.8 \pm 1.5$	$S_i = 3.2 \pm 0.2$ $S_c = 3.4 \pm 0.3$

Values are means ± SE.

CONTRAST. To assess the relationship between mean firing rates and oscillatory discharge in cortical cells, gratings of varying contrast were presented monoptically and dichoptically to 66 binocular cells. In these experiments the response selectivities to orientation, spatial frequency, and interocular phase were initially evaluated at 20% contrast in the interleaved manner described previously. Gratings of nine different contrast levels, typically from 1 to 20%, were presented either monoptically or dichoptically, for a total of 27 conditions. The contrast levels, as well as the eye or eyes to which the gratings were presented, were randomly interleaved. Because the response rates of cortical cells are directly related to contrast levels in the stimulus, these tests provided regular response strength increments. The contrast range was chosen to contain the contrast threshold of a given cell. Because of this, many responses had firing rates at or near those of spontaneous activity.

Among the 26 cells in this group that exhibited oscillations, 15 cells displayed the strongest oscillations under monoptic, as opposed to dichoptic, stimulation. By contrast, only 19 out of 98 cells showed a monocular preference in the comparison of binocular and monocular responses mentioned previously (see Fig. 9). This discrepancy is probably due to the different contrasts used: the vast majority of the previous comparisons of monoptic and dichoptic responses was made with the use of stimuli at 50% contrast. Thus monocular oscillations tend to be stronger than binoc-

ular oscillations at low, but not at high contrasts. In one case a cell's strongest oscillations were observed under the null stimulus condition, when completely demodulated gratings (0% contrast) were presented to both eyes. Responses did not show a consistent relationship between monocular or binocular contrast levels and oscillatory S/N ratios. In fact, only 4 of 26 cells exhibited oscillations at >3 of the 27 conditions studied.

To determine whether oscillations are only detectable for suprathreshold activity, monocular and binocular contrast thresholds were computed on the basis of the distinguishability of contrast responses from spontaneous activity. Receiver operating characteristic (ROC) analysis was used to compute the incidence of a response exceeding the null response (Green and Swets 1966; Tolhurst et al. 1983). A sigmoidal function was fit to these incidences, and the contrast at which the fitted curve intersected with 75% incidence was defined as the contrast threshold. This procedure was carried out separately for the left eye, right eye, and binocular responses. For the 26 oscillatory cells, the contrast threshold for the ocular condition (left, right, or both) at which the strongest oscillation was observed was used as the basis for comparison. The strongest oscillations were at contrasts above threshold for 16 cells, below threshold for 8 cells, and within 1% of threshold for 2 cells. Mean frequencies (45.7 and 38.7 Hz) and S/N ratios (3.7 and 3.5) were not significantly different for the below and above threshold oscillations.

Given the lack of any clear relationship between contrast levels and oscillations, all examples of oscillatory discharge were grouped together to study the possible relationship between mean firing rates and oscillatory S/N ratios for low-contrast stimuli. These data, summarized in the scatter plot of Fig. 13, suggest an inverse relationship between mean firing rate and oscillatory strength: only at lower firing rates were very strong oscillations observed. For example, 17 of the 19 responses in which the S/N ratio was >5.0 had mean firing rates of <20 spikes/s. This relationship probably explains the predominance of strong monocular oscillations, given that at low contrast levels, monocular responses are weaker than binocular responses.

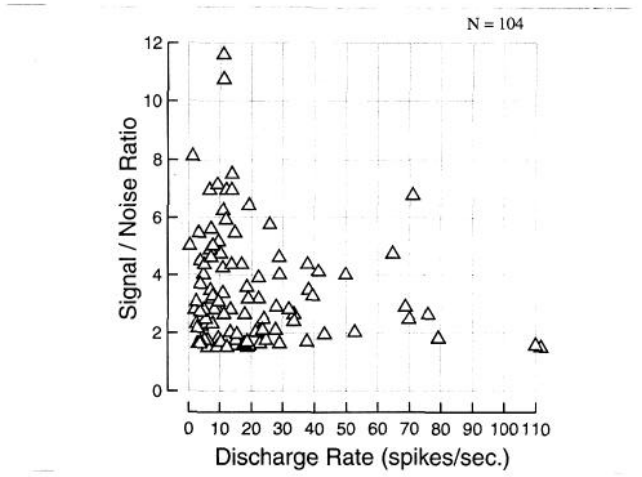

FIG. 13. Oscillatory strength is plotted vs. mean firing rates for 104 low-contrast (<20%) conditions. Included among these points are both monocular and binocular responses for 26 cells. The clustering of points in the *bottom left* demonstrates an inverse relationship between the incidence of strong oscillations and firing rate.

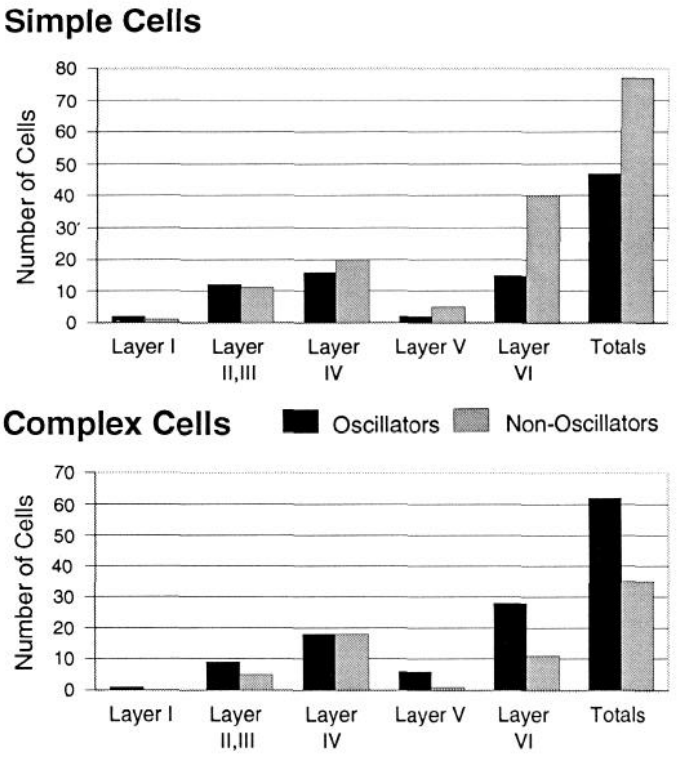

FIG. 14. Numbers of oscillatory and nonoscillatory cells are categorized according to laminar position and cell type. Differences between the oscillatory incidence of simple and complex cells (Totals) are largely due to differences within layers V and VI.

Laminar analysis

Laminar data are available for 124 of the 169 simple cells and 97 of the 166 complex cells. Of this population, 47 simple and 63 complex cells exhibited oscillatory discharge. Figure 14 shows the laminar distribution of oscillatory and nonoscillatory simple and complex cells. The majority of cells recorded were from layers 4 and 6. The ratios of oscillatory to nonoscillatory cells are similar for simple and complex cells in layers 1 through 4. When the supragranule layers are grouped together, we find a significant difference between the laminar distributions of oscillatory incidence for simple and complex cells ($\chi^2 = 37$, $P \ll 0.001$). This difference between simple and complex cells is due primarily to differences in layers 5 ($\chi^2 = 8$) and 6 ($\chi^2 = 28$). In layer 6, only 27% of simple cells are oscillatory ($n = 55$), whereas 72% of complex cells exhibited oscillatory discharge ($n = 39$).

From examination of the laminar distribution of all oscillatory cells, we find no laminar biases other than those present in the total sample. The distribution of simple-cell oscillators is statistically indistinguishable from the distribution of all simple cells ($\chi^2 = 4.0$; $P = 0.14$). This result also holds for complex cells ($\chi^2 = 1.8$; $P = 0.40$), and for simple and complex cells grouped together ($\chi^2 = 1.2$; $P = 0.75$).

Physiological cell type and the incidence of oscillations

Figure 15 shows the distribution of oscillatory strengths and frequencies exhibited by the 178 cells whose discharge was oscillatory, as judged by a S/N ratio greater than 1.5. Because only the strongest oscillation of each cell is plotted here, the data shown represent oscillations under a variety of stimulus conditions and durations for both kittens and cats. No oscillations were observed above 67 Hz with the exception of those due to screen flicker. Examination of the seven strongest cortical oscillators (S/N, >8.0) reveals only one neuron (a simple cell) whose oscillations are at a frequency greater than 37 Hz. No strong oscillations (S/N, >8.0) were found in either the LGN or the visual cortex between 40 and 50 Hz.

The incidence of oscillations among standard complex cells is higher (49%) than the incidence among simple cells (35%). On the basis of the laminar data presented in Fig. 14, this difference is due largely to differences in incidence within layers 5 and 6. This difference between simple and complex cells does not depend on the S/N criterion used for oscillation classification. If, for example, the S/N criterion is doubled to 3.0, 45 complex cells (27%) and 30 simple cells (18%) would be classed as oscillators.

Oscillatory frequencies and strengths for simple and complex cells show considerable overlap. In Fig. 16, distributions of oscillation frequencies are compared for 53 simple and 62 complex cells in the adult cat. These frequency distributions are statistically different ($\chi^2 = 22.4$ with 5 degrees of freedom, $P < 0.001$). The largest component of this difference comes from the 28- to 32-Hz range ($\chi^2 = 16.9$) in which oscillations are much more likely to occur among complex cells than simple cells.

The strongest oscillations for the entire population that we studied are seen among 10 LGN cells (8 Y-cells and 2 X-cells). The oscillations for this group are an order of magnitude stronger than those of cortical cells. Moreover, in contrast to the cortical oscillations, these oscillations are very stable. All of these cells have large spontaneous rates of activity, between 20 and 40 spikes/s. Oscillations are present in both spontaneous activity and stimulus independent. Because of this, the S/N ratio of LGN oscillations *decreased* with increased levels of stimulus-evoked discharge. Finally, although LGN cells show a range of oscillatory frequencies similar to that seen among cortical cells, all LGN oscillations with S/N ratios greater than 10 are found to have frequencies between 53 and 61 Hz.

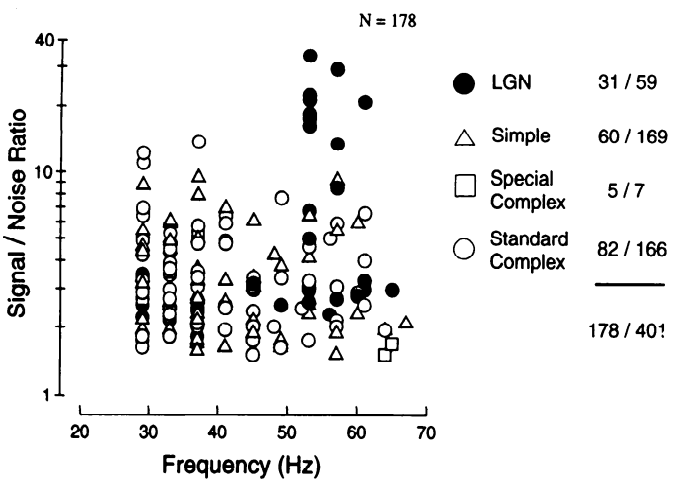

FIG. 15. Signal-to-noise ratios and frequencies of oscillatory discharge are summarized according to cell type. Of the lateral geniculate nucleus cells studied, 10 out of 59 showed stable oscillatory discharge that was stimulus independent. This group of cells, seen in the *top right corner*, has signal-to-noise ratios that are an order of magnitude larger than those typically seen over brief periods of time with cortical cells. The frequency range and single-to-noise ratios among simple and complex cell oscillators are similar.

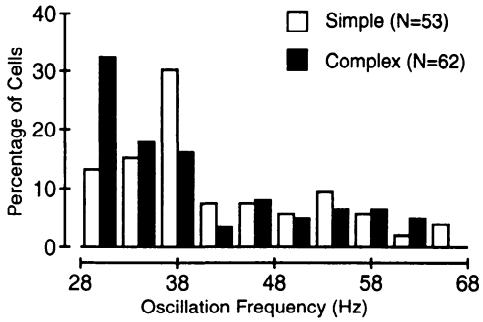

FIG. 16. Distribution of oscillation frequencies is different for simple and complex cells in the adult cat. Each bin represents a 4-Hz bandwidth of frequency. Note the large difference in the lowest frequency range (28–32 Hz), in which complex cells are most likely to be found.

DISCUSSION

We have studied the nature of oscillatory discharge from single cells in the LGN and striate cortex. Within the cortex, such discharge is variable with respect to frequency, strength, and timing relative to stimulus onset. In contrast, certain LGN cells display remarkably strong oscillations in the 50 to 60-Hz range. The presence of cortical oscillatory discharge is independent of the coherence and contrast of visual stimulation. The nature of oscillations is not dependent on whether the stimulation is monoptic or dichoptic. Oscillation strength in the cortex is constrained by discharge rate such that strongest oscillations are present in the weakest responses. Complex cells are more likely to be oscillatory than simple cells, especially in the midfrequency range around 40 Hz. Furthermore, there are developmental differences in this frequency range in that midrange oscillators are rarer in the kitten than in the adult. When all frequencies between 30 and 80 Hz are examined, oscillatory discharge does not have a laminar bias nor is it restricted to physiological cell types within the visual cortex.

Stimulus dependence

Models of oscillatory activity in the visual cortex have been developed with variability as a key component (Eckhorn et al. 1988; Gray et al. 1992a). For example, Gray et al. (1992a), observing the variable phase and short duration of local field-potential oscillations, have proposed that such variability is an important substrate through which rapid pattern recognition takes place. This proposal assumes that oscillations are stimulus dependent, which our single-cell data do not support. However, even if a stimulus

dependency exists among single cells or populations of neurons, variability places a limit on the reliable discrimination of oscillatory responses. For an ideal observer looking at a pattern of activity, variability limits the amount of stimulus information that can be conveyed by oscillations, because there is little consistency between the pattern and stimulus features. It is difficult to suggest that oscillations could be strictly encoding visual parameters, given that the oscillations are neither reliable in relation to the stimulus nor consistent with respect to duration, frequency, and strength.

Although our data contain no evidence for stimulus dependencies, it is possible that single-cell oscillations are dependent on attributes not tested here. Cortical cell sensitivity to parameters such as stimulus orientation, spatial frequency, binocularity, and contrast is well established with the use of the metric of mean firing rate. It is possible, however, that oscillations are dependent on visual parameters that do not affect firing rate. Such an open-ended scenario is very difficult to study unless a model provides guidance as to what stimulus dependencies to examine or unless some extant data suggest stimulus dependencies. After the trigger feature hypothesis (Barlow 1972), that the presence of strong firing enables the conveyance of information, a logical way to look for such dependencies is to examine attributes that have been implicated as functionally significant on the basis of firing rate selectivity. As shown here, no such data exist; nor is there any convincing model pointing to a testable stimulus dependency. Moreover, the inverse relationship between firing rate and oscillation strength shows that oscillations are most detectable when there is less, rather than more, neural discharge. This relationship is similar to that seen in single cells within the somatosensory cortex of an alert monkey (Ahissar and Vaadia 1990). For these oscillatory cells, oscillations were only present in the spontaneous activity; they were completely suppressed with effective tactile stimuli.

In the only previous systematic study of binocularity and oscillations, Gray et al. concluded, on the basis of 9 out of 16 recordings, that binocular stimulation enhances oscillatory responses (Gray et al. 1990). Because this study used drifting bars for visual stimulation, a temporal overlap of PSTH records was used to align receptive fields for the two eyes. This method was only partially successful; 10 out of 26 cells showed no temporal overlap. The Gray et al. experiments, in contrast to the interocular phase experiments conducted here, were also unable to systematically vary binocular stimulation. Another complication is the small sample size, which, because of oscillatory variability, constrains any generalization of their findings. The importance of sample size is borne out by the fact that the Gray et al. study finds no cells for which monocular oscillations are stronger than those occurring under binocular stimulation. For our sample of 98 cells, 38 cells showed stronger oscillations under binocular stimulation, whereas 34 cells showed just the opposite. The finding here concerning the lack of any relationship between interocular phase and oscillations makes it additionally unlikely that oscillations could serve to encode binocular information.

The dependence of oscillations on the coherence of visual stimuli is relevant to models in which these oscillations serve to link visual features. The data of our study have been obtained from a large sample size by the use of sinusoidal gratings, which are truly coherent stimuli of single spatial and temporal frequencies. It is also possible that the 20-Hz signal, which is present in the incoherent stimuli because of the regularity of bar presentation, can influence oscillatory discharge. It is unlikely, however, that the oscillations observed are a direct result of the 20-Hz signal because shuffle subtraction was performed, and (as shown in Fig. 12) that there is no particularly tendency for oscillatory frequencies to be clustered around the harmonic frequencies of 20 Hz (i.e., 40 and 60 Hz). Our results suggest that neither the incidence of oscillatory discharge nor the strength of oscillations depends on the coherence of visual stimuli.

When attempting to reconcile the current data with those published previously, it is important to keep in mind the fundamental differences in the methods of analysis. As shown in Fig. 4, the method of fitting damped sinusoids (Gabor function) has its limitations. According to the criteria of previous studies, an autocorrelogram is indicative of oscillations if the amplitude of this fitting function exceeds the standard error of the fit by a factor of two or more (Gray and Singer 1989; Engel et al. 1990a). Another method used was to measure the modulation of the initial peak and trough within the autocorrelogram (Gray et al. 1990). Both of these techniques fail to quantitatively measure oscillation strength relative to noise. This introduces possible ambiguity into comparisons between different cells and different stimulus conditions. A spike train classed as oscillatory on the basis of the fit of a 1-cycle sinusoid can be classed as nonoscillatory with the use of the power spectra method. A spike train containing pairs of spikes of a specific interspike interval might not contain a consistent series of these pairs. By emphasizing the first peak of the autocorrelation function, previous fitting methods would lead to the classification of this spike train as oscillatory even though its autocorrelogram is bimodal and not multimodal.

Another analytic difference is the subtraction of shuffled autocorrelograms. Because no periodicities were found in shuffled autocorrelograms, previous investigators judged these correlograms to be inconsequential (Gray and Singer, 1989) and performed curve fitting without shuffle subtraction. However, even if shuffled autocorrelograms contain no periodicities, they can still reveal stimulus-locked effects that would alter the nature of periodicities in raw correlograms if subtracted. For example, a noisy shuffled autocorrelogram could increase the amount of noise when subtracted from the raw autocorrelogram. Thus oscillation analysis based on autocorrelograms without shuffle subtraction is potentially inaccurate.

An experimental difference between the current study and previous investigations of cortical oscillations is the use of CRT monitors to provide visual stimulation. Previous studies have generally used bar stimuli illuminated by a DC light source (Gray and Singer 1989; Gray et al. 1990; Engel et al. 1991a,b). This raises the possibility that the flicker rate of our CRT displays somehow modifies the oscillatory behavior of the neurons we studied. For several reasons, we believe it is unlikely that the high-frequency signal associated with CRT flicker affects oscillatory discharge. First,

although cells within the LGN are able to respond to the refresh rate of our CRTs (76 Hz), cortical cells seldom respond to temporal frequencies above 10 Hz. Furthermore, any direct effect of CRT flicker on neuronal discharge is eliminated by shuffle subtraction (see Fig. 2). As shown in Fig. 15, very few cells, after shuffle subtraction, exhibit any oscillations at frequencies above 60 Hz, and many strong oscillations are seen at ~30 Hz. Although low-frequency signals can create high-frequency harmonics, the 76-Hz frequency of CRT refreshing could affect the lower frequency oscillations studied here only in the presence of gross temporal nonlinearities. If such nonlinear mechanisms are commonplace, then CRT flicker should cause an increase of low-frequency discharge in a large proportion of cells for all conditions because CRTs were used in all the tests described here. However, no such consistency was observed. Because each trial was locked to CRT refresh, even if nonlinear mechanisms behaved in a variable fashion, their effects should be locked to stimulus presentation and therefore be eliminated by shuffle subtraction. Finally, because oscillatory activity was observed among certain cells, CRT flicker clearly does not eliminate oscillatory discharge. Although CRT flicker could still affect the stimulus dependence of oscillations without altering the frequency or variability of the oscillations themselves, there is no evidence that stimulus dependencies, as measured by the metric of firing rate (e.g., in the case of contrast sensitivity), are affected by the use of CRT monitors.

Despite the differences between the methods of our study and those of previous investigations, the nature of oscillatory discharge reported here is, in some respects, consistent with previous studies. For example, the frequency range of oscillations and the incidence of oscillations among complex cells is in general agreement with a previous study examining the relationship between receptive-field type and the incidence of oscillation (Gray et al. 1990). This suggests that, despite the arbitrary nature of the criteria used in both the power spectra and Gabor function methods, there is general agreement concerning the physiological and laminar occurrence of oscillatory cells. It also suggests that oscillatory discharge is not likely to be generated by or severely disrupted by the high-frequency flicker of CRT monitors.

Physiological cell type and location

There is a dramatic difference, however, between our results and those previously reported concerning the incidence of oscillations among simple cells. In the study of Gray et al., only 12% of simple cells are oscillatory (Gray et al. 1990); our data indicate that 36% of simple cells can show oscillatory discharge. In the previous work the spatial overlap of ON and OFF regions as revealed by manually controlled bars was used, as opposed to the degree of modulation to sinusoidal gratings, as the basis for distinguishing between simple and complex cells. However, differences in the method of receptive-field classification cannot totally account for this discrepancy because the total incidence of oscillations among all cortical cells is also different. In the Gray et al. study, 39 out of 143 cells were found to be oscillatory (27%), whereas in the current study 147 out of 342 cortical cells were classed as showing some oscillation (43%). Although this difference is not enormous, it is difficult to explain given the fact that the lack of shuffling and the emphasis on the primary peaks of autocorrelograms are likely to lead to oscillatory classifications in cases where the power spectra method does not, and would therefore result in higher incidences of oscillatory activity being reported. One possibility is that methods that emphasize a single interspike interval are insensitive to oscillations when the firing rate is low and therefore lead to underestimates of oscillatory incidence.

The difference in the incidence of oscillatory discharge among simple cells probably accounts for the discrepancy between the laminar distribution shown here and that of a previous study (Gray et al. 1990). In the previous study, only 2 out of 15 cells in layer 4, and 7 out of 27 layer 6 cells were oscillators, whereas in this study 34 out of 72 layer 4, and 43 out of 94 layer 6 cells exhibited oscillations. Finally, no data are presented in the previous study to distinguish the laminar distribution of simple and complex oscillatory cells.

Although the sample size is limited in our study, the prevalence of oscillations within layer 5 is consistent with the previous laminar report. In our study, six out of seven complex cells show oscillatory discharge, and five of these oscillate at 29 Hz. These low-frequency oscillations can be very strong, ranging up to 12.2 in signal to noise. These findings are particularly interesting given the finding of lower frequency spontaneous oscillations within layer 5 (Silva et al. 1991).

Differences in analysis or classification also fail to account for the discrepancy in the LGN data. Several investigators have reported oscillatory cells in the LGN (Arnett 1975; Bishop et al. 1964; Munemori et al. 1984). Both the percentage of oscillatory cells and the nature of the discharge seen in our study are consistent with these previous reports. For example, previous studies found these oscillations to be a characteristic of spontaneous activity, which is stimulus independent. Given that all studies report a relatively small incidence of these oscillatory cells among the LGN population (around 20%), Gray and Singer's failure to find such cells might be due to minimal sampling. Gray and Singer do not mention how systematically, or for how many cells, LGN firing was examined (Gray and Singer 1989).

Bishop et al. (1964) first suggested that the oscillations seen in the LGN reflect spontaneous oscillations within the retina. Spontaneous oscillatory discharge among rabbit and cat retinal ganglion cells has been observed in several studies (Ariel et al. 1983; Barlow et al. 1964; Kuffler 1953). A subclass of retinal ganglion cells in the cat, called Q-cells, which are similar in physiological properties to Y-cells, display strong coherent oscillations in the same frequency range as those observed in the LGN (Robson and Troy 1987). These oscillations are quantitatively identical in terms of S/N to those observed in the LGN (unpublished observations). Oscillations in the LGN could potentially be traced back to amacrine cells, given that certain amacrine cells of the catfish retina produce spontaneous oscillations at ~35 Hz in frequency (Sakai and Naka 1990) and that amacrine cells are thought to contribute oscillatory potentials in the mudpuppy retina (Wachtmeister and Dowling

1978). It is also possible that the LGN oscillations observed here might largely reflect the intrinsic oscillatory properties of certain LGN cells.

Are cortical oscillations driven by LGN oscillations?

Given the strength of the LGN oscillations, models that depend on the absence of geniculate oscillations must be questioned. Several models relying on intracortical interactions require rather specific patterns of connectivity (Cotterill and Nielsen 1991; Eckhorn et al. 1989; Grossberg and Somers 1991; Schuster and Wagner 1990; Sporns et al. 1989). Additionally, these models are based on notions of stimulus encoding that seem unlikely given the current evidence. A much simpler model is one in which extrinsic oscillations from the LGN are primarily responsible for the oscillations seen within the cortex, as shown in Fig. 17.

Variable oscillations in the cortex would arise if oscillations of LGN cells are independent or weakly dependent on each other. The stimulus independence of LGN oscillations would, in turn, result in stimulus-independent cortical oscillations. In the model illustrated in Fig. 18, a pair of nearby cortical cells oscillate when an appropriate number of their LGN inputs are oscillating. The strength of cellular oscillations is depicted in this figure by the spreads seen in the interspike interval distributions. For strongly oscillatory cells, intervals between successive spikes vary around a mean interval that is the inverse of the oscillation frequency. LGN cells oscillating at 50 Hz therefore have a narrow distribution of spike intervals centered around 20 ms. If the interspike intervals from each of these oscillatory cells vary over time independently, each cell's discharge can be considered an independent random process. A cortical cell that discharges according to the sum of its LGN inputs

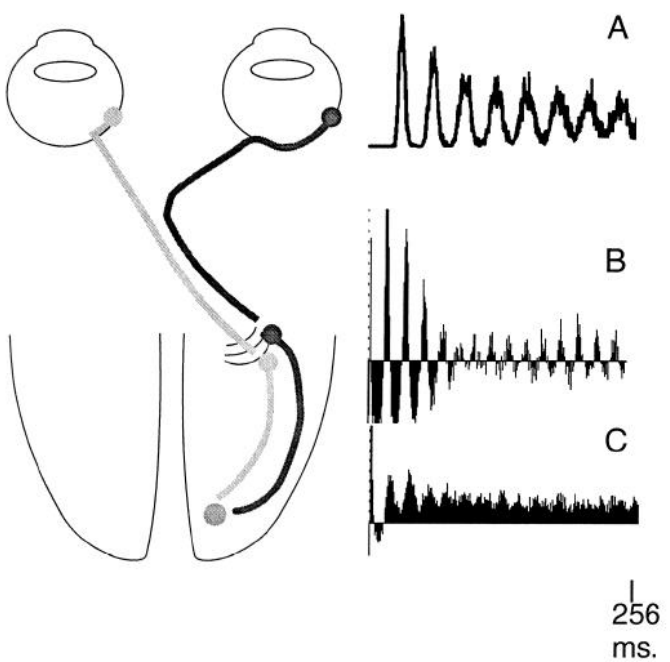

FIG. 17. Oscillations originating from the spontaneous activity of a subpopulation of cells in the retina propagate through the central visual pathway. Autocorrelograms on the *right* were obtained from single-unit recordings in the retina (*A*) (Robson and Troy 1987), lateral geniculate nucleus (*B*), and visual cortex (*C*).

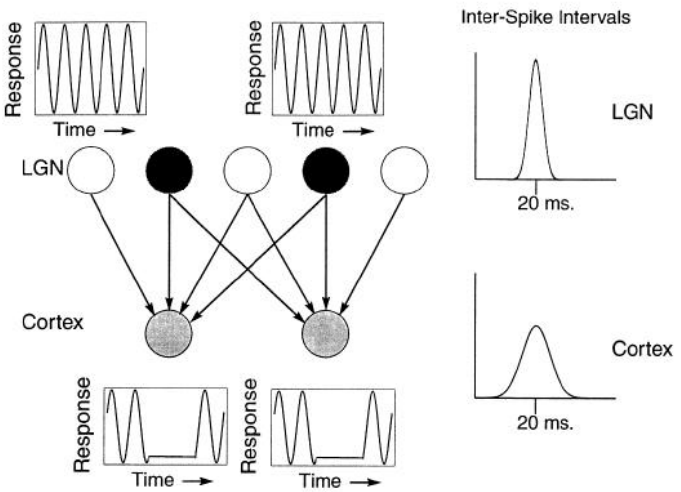

FIG. 18. In this model, oscillatory lateral geniculate nucleus (LGN) cells are responsible for cortical oscillations. Cells in the LGN either oscillate independently (black circles) or do not oscillate (white circles). Bandwidth of the interspike interval histogram reflects the consistency and coherence of oscillatory discharge. In this model the narrow range of interspike intervals seen in the *top right* reflects the coherent 50-Hz oscillation of a single LGN cell. The broader spread of interspike intervals exhibited by a cortical cell is shown in the *bottom right*. Cortical cells (gray) are less coherent oscillators because their responses are governed by the integration of asynchronous oscillatory inputs (black) and non-oscillatory inputs (white). Oscillations of the 2 cortical cells are synchronized because they receive common oscillatory input.

would therefore exhibit weak oscillations because the variance of the sum is larger than that of any individual input. Because of the retinotopic organization of geniculate afferents, nearby cortical cells would tend to receive the same pool of oscillatory input and therefore would oscillate in phase with one another.

Such a model is only feasible if nearby LGN oscillations are not tightly coupled. We have observed nonsynchronous discharge between two oscillatory LGN cells recorded from the same electrode. Cross-correlation analysis of the discharges reveals that one cell tended to fire 4 ms after the discharge of the other cell. Because both cells oscillated at a frequency of 53 Hz, one cycle of oscillation was 19 ms in duration. The two neurons therefore oscillated with a temporal phase difference of 76°. Asynchronous oscillations were also seen by Arnett in the cross-correlation analysis of the discharge of two LGN cells with overlapping receptive fields (Arnett 1975). These neurons oscillated with a temporal phase difference of 36° (2 ms over 20 ms/cycle). Given such asynchrony, there would be only brief periods in which multiple geniculate oscillators could provide input sufficiently in phase to evoke rhythmic cortical discharge.

LGN oscillations are independent of visual stimulation, and therefore their effects on the cortex are also stimulus independent. Oscillations are not observed in the normal spontaneous activity of cortical cells because of the very low rates of spontaneous activity seen in the cortex. However, once the stimulus strength is raised just enough to evoke neural firing, as in the contrast experiments of our study, oscillations become apparent. These oscillations become weaker as the stimulus strength is raised because of the great contribution of visually dependent input to the cortical discharge. One possible explanation is that spontaneous

subthreshold oscillations exist within neurons whose influence on discharge is only visible when the threshold is reached by visual stimulation.

It is also possible that neurons with intrinsically oscillatory properties contribute to the oscillations observed here. Cortical neurons with intrinsic oscillatory properties have been observed in several intracellular studies. Intracellular recording of neurons within layer 4 of guinea pig frontal cortex slices has revealed the presence of subthreshold oscillations in the 10 to 45-Hz range (Llinas et al. 1991). Thalamocortical cells can also exhibit subthreshold oscillations between 20 and 40 Hz when appropriately depolarized (Steriade et al. 1991). In both cases these oscillations can give rise to action potentials. Thus it is possible that intrinsic oscillators exist at all levels of the visual system, from retina to cortex. One dramatic example of intrinsic oscillatory activity is found in layer 5 pyramidal neurons of mouse cortex, in which 5- to 12-Hz rhythmic firing for periods up to 20 s can be triggered by spontaneous or evoked postsynaptic potentials (Silva et al. 1991). The intrinsically oscillatory nature of certain cortical cells might be responsible for many instances of oscillatory discharge. This is especially true for those cells that oscillate at ~30 Hz in frequency (unpublished observations).

Oscillatory synchrony

If LGN cells are the primary source of cortical oscillations, the greatest oscillatory synchrony should be observed within small cortical areas. This is because cells in retinotopic proximity are the most likely to share geniculate inputs (Tusa et al. 1975). A recent study of the synchrony of oscillations over different cortical distances showed that distance, rather than similarity of orientation sensitivity, is the strongest determinant of rhythmic synchrony (Engel et al. 1990a). The largest proportion of synchronous oscillations occurred for cells within 2 mm of each other, and, for cells within this distance, the similarity of orientation selectivity had no effect on the chances of synchronous discharge. This is the same distance as the cortical divergence of a single point from the LGN, as determined histologically by anterograde staining (Salin et al. 1989). Given the relatively local nature of oscillations, the divergence of LGN input to the cortex likely provides the most parsimonious mechanism for synchronous oscillations over small distances.

There are cases for which oscillatory synchrony, or any synchrony for that matter, is clearly dependent on intracortical connections. For example, synchronized interhemispheric oscillations have been observed (Engel et al. 1991a) despite a conduction delay of ~4 ms across the corpus callosum (Harvey 1980). One possibility is that inhibitory interneurons contribute to synchronization (Crick and Koch 1990). Appropriate combinations of excitatory short-range and long-range interactions will also synchronize oscillatory cells (Sompolinsky et al. 1990). However, the fact that cortical circuitry exists that influences synchronous firing within the cortex does not necessarily imply that oscillations themselves are generated within the cortex. For example, oscillations could be generated precortically and propagated to the cortex, where intracortical connections (Schwarz and Bolz 1991; T'so et al. 1986) could synchronize oscillations across large distances. Horizontal sectioning of mouse cortex slices reveals that layer 5, where such long-range connections can be found, is both necessary and sufficient to produce synchronized oscillations in other layers (Silva et al. 1991).

Oscillation frequencies

Engel et al. reported a unimodal distribution of frequencies seen in multiunit discharge around 50 Hz, with very few oscillations below 40 Hz or above 60 Hz (Engel et al. 1990a). This is in contrast to the single-unit data presented here, which show a broad distribution of oscillatory frequencies. One possibility is that nearby cells, such as would be recorded from a multiunit electrode, are less likely to oscillate in phase at these lower frequencies. Multiunit activity does not necessarily reflect single-unit discharge; peaks can arise both from the discharge of individual neurons and the summation of potentials produced by several neurons simultaneously. For example, rhythmic activity can be seen at a frequency of 300 Hz in multiunit recording but not in single-unit recording in the extrastriate cortex (Reinis et al. 1988). Another possibility is that, because bars are more incoherent than gratings, the data of Engel et al. more closely correspond to that of reverse correlation data than to data obtained with the use of gratings. The mean oscillatory frequency of 49 Hz reported in the Engel et al. study more closely matches the mean seen with incoherent stimuli (47 Hz) than it does the mean seen with coherent stimulation (38 Hz). The relative inability of bars to evoke low-frequency oscillations might explain these differences in frequency distribution.

The difference in oscillatory frequencies that we have found between kittens and cats could be explained in two ways by the LGN model described above. The immaturity of neurotransmitter distribution (Shaw et al. 1986) and efficacy (Tsumoto et al. 1987) in kittens could affect cortical cell firing thresholds or the integration of geniculate inputs. Additionally, the relative immaturity of geniculate afferents could change the distribution of input that cortical cells receive (Kato et al. 1983; Tsumoto and Suda 1982). One important point is that, although the nature of oscillations changes with development, the existence of oscillations is not dependent on postnatal maturation. This has been confirmed by local field-potential recordings from the kitten's visual cortex (Gray and Singer 1989). This suggests the possibility that strong oscillations might be present in the retina and LGN of 4-wk postnatal kittens just as they are in the adult. Although spontaneous activity has been observed prenatally in the rat (Galli and Maffei 1988), the developmental time course of the intrinsic oscillations described by Robson and Troy (1987) for the cat retina is unknown.

Potential functional roles of oscillatory activity

The incidence of oscillations among different cell groups as well as the strength and frequency of these oscillations can be accounted for by a model that relies on the nature of LGN input to the cortex (unpublished observations). By incorporating the oscillatory discharge of the LGN, LGN divergence, and the existence of intrinsic oscillators within the cortex, oscillations in cortical discharge that are consistent with the data can be generated without any reliance on intracortical connections. It should be noted that, even if

cortical networks are not responsible for the generation of oscillations, oscillations might still play an important functional role. For example, Crick has suggested that rapid bursting in the geniculate might serve as an internal attentional spotlight that scans over the representations of objects in the cortex (Crick 1984). It is possible that the oscillations observed in the LGN play a role in visual attention or awareness that cannot be revealed in an anesthetized preparation (Crick and Koch 1990). For example, 36-Hz waves seen in the electrocorticograms of behaving cats are dependent on levels of attention and noradrenergic activity (Delagrange et al. 1989). If oscillations are highly dependent on alertness, then differences in anesthesia protocols might help explain the differences in oscillatory incidence mentioned previously, because Gray et al. used halothane as their anesthesia, as opposed to Surital and N_2O (Gray et al. 1990).

Oscillations within an appropriately connected network in primary visual cortex could provide a means for higher order neurons to segregate features (von der Malsburg and Schneider 1986). In this manner extrastriate cortical networks might modify or modulate these oscillations to encode information. There is, however, uncertainty over whether synchronized oscillatory discharge would be particularly effective in coding features. Although von der Malsburg and Schneider proposed a scheme in which burst synchronization provides a means of segregating auditory patterns (the "cocktail-party effect"), their scheme does not explicitly depend on the presence of rhythmic discharge (von der Malsburg and Schneider 1986). In fact, a simulation of oscillatory patterns in the visual cortex indicates that coding or segregating visual features on the basis of oscillation phase would lead to many ambiguous classifications (Noest and Koenderink 1991). One potential problem in trying to encode features with oscillations that are distributed over large cortical regions is that oscillations of the same frequency but different phases are likely to either cancel one another or to completely synchronize (Crick and Koch 1990).

Oscillatory spontaneous activity in the retina could also provide cues for activity-dependent refinements within the developing visual system. It has been shown that the suppression of retinal activity through tetrodotoxin injection can prevent eye-specific segregation within the LGN (Sretavan et al. 1988) and ocular dominance column segregation within the cortex (Stryker and Harris 1986). Spontaneous activity has been shown to be correlated between nearby cells in the immature rat (Maffei and Galli-Resta 1990) and ferret retina (Meister et al. 1991). Furthermore, low-frequency bursting activity has been observed in the LGN of immature rabbits (Rapisardi et al. 1975). If oscillations in retinal spontaneous activity are present prenatally, they could therefore serve as a very stable signal for refining the connections in LGN and cortex. In this case, oscillations observed in the mature animal may simply be the remnant of a developmental process.

The attentional and developmental significance of oscillations in the central visual pathway can be explored with further experiments. The set of experiments described here has focused specifically on the potential of cortical oscillations to convey visual information and on the mechanism by which oscillations are generated. The stimulus independence and inverse firing rate dependence of oscillations in the LGN and visual cortex suggest that oscillations in single-unit discharge may be an epiphenomenon of retinal spontaneous activity and may not depend on properties of visual stimulation.

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