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Oscillatory Firing and Interneuronal Correlations in Squirrel Monkey Striate Cortex

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SUMMARY AND CONCLUSIONS

1. This work explores a mechanism that the brain may use for linking related percepts. It has been proposed that temporal relationships in the firing of neurons may be important in indicating how the stimuli that activate those neurons are related in the external world. Such temporal relationships cannot be seen with conventional receptive field mapping but require cross-correlation and auto-correlation analysis.

2. In the cat and the macaque monkey, cells with similar receptive field properties show correlated firing even when their receptive fields do not overlap. Here I report that in the squirrel monkey, as in the cat, pairs of cells ≤5 mm apart can show correlated firing, and these correlations between pairs of cells are often stronger when they are stimulated by a single contour. This suggests that the correlations reflect not only permanent connections between cells with similar receptive fields, but in addition may encode information that the activating stimuli are continuous or part of a single object. I also find that, as in the cat, and contrary to some other reports on experiments in monkeys, the correlated firing is often rhythmic. These recordings further indicate that periods of rhythmicity are associated with stronger interneuronal synchrony, which is consistent with the hypothesis that recurrent feedback loops are involved in generating both.

3. Pairs of cells in the same cortical column, but at different depths also showed correlated firing, but with several milliseconds difference in timing between layers. This was true for cells at different depths within layer 2/3 and for pairs of cells in different layers (2/3 vs. 4B or 4Cα), providing evidence for cross-talk between the magno- and parvocellular streams.

INTRODUCTION

One of the most important tasks in perception and cognition is deducing that two pieces of information are related and then linking them together. The Gestalt psychologists recognized that the visual system automatically links together related parts of the visual scene, and it has often been suggested that this is accomplished by the convergence of inputs from neurons at early stages, whose receptive fields are tiny, onto neurons in sequentially higher visual areas, where receptive fields are larger but generally more complicated. Visual cortex comprises at least 25 richly interconnected areas (Felleman and Van Essen 1991). In the primate, visual information feeds first into Visual Area 1 (V-1), and from there to sequentially higher visual cortical areas. These higher visual areas do not form a single hierarchical pathway but are arranged in several parallel systems within which areas are mostly hierarchically connected. Each system ultimately feeds into polymodal association areas (for reviews see Felleman and Van Essen 1991; Morel and Bullier 1990; Van Essen 1985).

Several important facts are inconsistent with the idea that visual perception emerges solely from activity in higher visual cortical areas by a stepwise, unidirectional analysis of information. First, sequential information processing in multiple stages could allow the elaboration of very complicated response properties but would create difficulties in retaining information about spatial location. For higher level cells to elaborate complicated response properties yet retain spatial information would seem to require a huge increase in the number of cells at each stage. But there is not; V-1 is by far the largest visual area. Indeed, cells in higher visual areas do not seem to retain spatial information—they generally have large receptive fields, often encompassing half or the entire visual field, even though precise spatial information is clearly accessible to our conscious perception. If information at all levels were accessible to perception then there would be no need to reiterate information at each stage, and the so-called "combinatorial explosion" that would otherwise result is avoided.

A second problem with a simple hierarchical model of information processing is that even though we perceive a single object as having a particular color and shape and precise location, anatomic and physiological studies indicate that different aspects of visual perception, such as form, color, motion, and stereoscopic depth, are carried by separate, relatively independent subdivisions of the visual pathway (Felleman and Van Essen 1991; Livingstone and Hubel 1988). These subdivisions are closely apposed in V-1, but more segregated in higher cortical areas (Maunsell and Van Essen 1983; Zeki 1974a,b, 1983). One might imagine that the interconnections between the various higher areas could integrate the information, but the large receptive fields pose a problem for precise reintegration. A more attractive possibility is that some linking between the different streams occurs in lower visual areas, where all the submodalities are closely interdigitated in a single high resolution retinotopic map. Within the primary visual cortex such horizontal connections indeed extend up to several millimeters and could therefore perform this integration (Gilbert and Wiesel 1979, 1983; Rockland and Lund 1983). Yet conventional visual field mapping does not reveal any physiological effects of these connections on the responsiveness of cells to stimuli.

An alternative to the hierarchical model is one in which dynamic networks of cells at many levels express relationships by temporal correlations. In such a model these long intra-areal connections could be involved in regulating firing *patterns* rather than firing *rate*, to generate the oscillations and interneuronal correlations I will be discussing. To integrate information from different levels would seem to require

bidirectional connections, and indeed, for each feedforward set of connections there is a strong reciprocal feedback pathway (see Felleman and Van Essen 1991). Yet a number of physiological studies have also failed to find any clear integrative role for these ubiquitous connections (Baker and Malpeli 1977; Geisert et al. 1981; Marrocco et al. 1982; Sandell and Schiller 1982; Schmielau and Singer 1977). Therefore for these inter-areal connections as well, one function may be in regulating firing patterns rather than absolute firing rate.

Studies on cat visual cortex using the technique of correlation analysis to focus on patterns rather than overall rates of firing have suggested such a role for the long intra- and interareal connections, and a possible way that temporal correlations might integrate information from different functional streams and between different levels. Ts'o and his colleagues (Ts'o et al. 1986; Ts'o and Gilbert 1988) used correlation analysis and found evidence for interactions between cells with non-overlapping receptive fields. Several groups in Germany, Gray and Singer (1989), Eckhorn et al. (1988), and Engel et al. (1990) looked at temporal patterns in the firing of single cells and groups of cells in cat visual cortex, and found that many cells fired rhythmically and that the firing of pairs of cells was often correlated. Gray and Singer and Eckhorn et al. found that many of the cells they recorded (50–70% of the neurons in the cat visual cortex) fired regularly spaced bursts of action potentials, and that these bursts tended to be synchronized for many cells within a local region. The synchronized firing occurs in response to a visual stimulus, but is not stimulus-locked (that is, it does not show any reproducible phase relationship to repeated stimulus sweeps) and therefore does not arise from some substructure of the receptive field. Rather it seems to reflect some network property of the interneuronal connectivity. Gray et al. (1989) and Engel et al. (1990) also observed synchronized firing between neurons that were up to several millimeters apart in the cortex and had nonoverlapping receptive fields; the correlations tended to be stronger if the two cells had similar orientation and direction selectivity. The synchronization between cells with nonoverlapping fields was particularly strong if a single contour, rather than two separate edges or a discontinuous contour, stimulated both fields simultaneously. Engel et al. (1991c) further observed synchronous oscillations between cells in two separate visual cortical areas, area 17 and area 18, and the correlations were strongest if the two cells were stimulated by a single contour. From this evidence, they have suggested that correlated firing may *link* together responses of cells activated by different parts of the same object, though they have tested responses only to parts of the same contour. Colinearity is, of course, one feature the visual system uses to link parts of an object (Rubin 1915), but it may be that other attributes of a single object will turn out to be perceptually linked by temporal correlations. In this study I have begun to ask whether similar phenomena occur in monkey striate cortex.

METHODS

Animal preparation

These physiological recordings were done entirely under surgical levels of anesthesia, and all experiments were acute. On the day of the experiment, the animal was first anesthetized with ketamine (15 mg/kg) while in its cage. The insertion of an intravenous catheter and an endotracheal tube were done under ketamine anesthesia, and then the anesthesia was switched to a 2% halothane in air mixture. Under halothane anesthesia, but before paralysis, the remaining surgical procedures were performed: fixation of the head, scalp incision, drilling a small hole in the skull, and attachment of the microdrive using dental impression compound.

All experiments were done according to the rules of the Harvard Medical School Standing Committee on the Use of Animals. The Harvard Medical School animal management program is accredited by the American Association for the Accreditation of Laboratory Animal Care, and meets National Institutes of Health standards.

Physiological recording

Before recording, administration of the paralyzing agent was begun (intravenous gallamine, 10 mg/kg, then 2 to 5 $mg \cdot kg^{-1} \cdot h^{-1}$). The level of anesthesia was monitored with an EEG (Model 79D, Grass Instrument) recorded from electrodes on the skull, to watch for any periods of desynchronization that might suggest the animal was getting close to arousal, and with an ECG rate meter to warn of tachycardia. We have monitored the EEG in anesthetized unparalyzed monkeys and find that as long as the EEG does not show prolonged desynchronization, the animal shows no signs of withdrawal to painful stimuli or spontaneous movement or vocalization. Exhaled CO_2 was continuously monitored with a Hewlett-Packard airway CO_2/O_2 patient monitor. Temperature was monitored and maintained with a water circulation heating pad. The eyes were fitted with contact lenses to focus them at 1.5 m, as determined with a Copeland Streak retinoscope. The relative positions of the two foveae were determined by using a reversing ophthalmoscope. The eyes were aligned with a Risley prism. Signals were recorded with arrays of enamel-coated tungsten electrodes glued together. Extracellularly recorded signals were amplified, filtered (0.3–10 kHz for the spikes and 20–200 Hz for the local field potential), and fed into a Brainwaves spike analyzing system with a 1-kHz sampling rate. Spikes were recorded as occurring when the recorded voltage crossed a preset threshold. Spike times were assigned with a 1-ms temporal resolution. At intervals during the recording small ($2\mu \times 2$ s) electrolytic lesions were made, to correlate the physiological properties of cells with their anatomic localization (Hubel 1957).

Visual stimuli

I used a color graphics system consisting of a Sharp XG-2000U liquid crystal video projector (or a Trinitron monitor in earlier experiments) and graphics equipment (Silicon Graphics Iris 3030 system).

Data analysis

AUTOCORRELOGRAMS. An Iris computer (Silicon Graphics 3030) was programmed to calculate auto- or cross-correlation histograms for single spikes, and the spike-triggered average of the local field potential. Patterns in the firing of single neurons were determined by calculating autocorrelograms exactly as described by Perkel et al. (1967a)—a histogram is accumulated of time differences (t) between each spike in the spike train within an interval T and the occurrence of every other spike within a given window of that interval, t.

CROSS-CORRELOGRAMS. Relationships between two cells were studied by calculating cross-correlograms exactly as described by Perkel et al. (1967b)—a histogram is accumulated of time differences (t) between each spike in an interval T in the first spike train and each spike in the other train within a time window, t. The first cell is arbitrarily considered the reference cell, and then

the left group of bins, the negative times, in the histogram represent times when the second cell fired before the reference cell. The center or zero bin shows the number of times when the two cells fired within 1 ms of each other, and the right bins indicate occasions when the reference cell fired before the second.

SHUFFLED CORRELOGRAMS. Perkel et al. (1967a) describe a method, shuffling, that determines which aspects of a correlogram are time-locked to the stimulus. In this technique the response intervals in a spike train are temporally offset by an integral multiple of the interstimulus interval before calculating the correlogram. I calculated trial-shuffled autocorrelograms for a series of responses in a single cell by accumulating a time difference histogram for each spike in one response compared with the next response in the series, then averaging the correlograms. Shuffled cross-correlograms are calculated between each response of cell 1 in a series and the subsequent response in cell 2, then the correlograms averaged. Any response series in which the shuffled auto- or cross-correlograms were not essentially flat for the 200- to 300-ms time interval calculated was not accepted for analysis. In most experiments, <2% of the cells showed nonflat shuffled correlograms, and in one experiment 30% of the cells showed oscillatory shuffled correlograms. That entire experiment was not included in the analysis.

CORRELATION INDEX. An index was calculated to measure the degree of correlation between a pair of cells: the size of the central peak of the averaged cross-correlogram (half the distance from peak to trough) was measured and divided by the height of the averaged trial-shuffled cross-correlogram. This measurement is illustrated for the left cell in Fig. 13; the full distance from peak to trough on the cross-correlogram and the height of the shuffled cross-correlogram are both indicated, and from these measurements a correlation index of 0.41 was calculated.

LOCAL FIELD POTENTIAL. The spike-triggered average of the local field potential is calculated by accumulating the average value of the field potential as a function of time difference, in 1-ms bins, from the occurrence of each spike in the spike train.

OSCILLATIONS. To ask how oscillatory each averaged autocorrelogram was, it was fit with a damped cosine wave by using a least squares fit. For each integral frequency between 30 and 100 Hz, the correlogram was multiplied by a cosine wave of that frequency, attenuated by 1-t (the attenuation allows infinitely fine temporal resolution). The frequency band ±1 Hz around the frequency giving the highest product was then explored at one-tenth of a hertz intervals to determine the frequency within this band giving the maximum product. If the maximum cosine wave × correlogram product was >4 SD larger than the average product for all the integral frequencies (30–100 Hz, excluding ±10 Hz around the optimum frequency), that correlogram was considered oscillatory and assigned that frequency. The frequencies ±10 Hz on either side of the maximum were eliminated from the comparison because a plot of frequency versus the correlogram × cosine wave products for 25 correlograms from real spike trains had broad maxima that were <20 Hz wide. We assume the values outside that range are random. We want to know how likely it is that the largest product would be 4 SD larger than the average of the products for 49 other frequencies. This is equivalent to asking how likely it is that the largest of 50 random numbers is four standard deviations larger than the average of the other 49. We calculate that the probability that this would happen by chance is <1% (see APPENDIX). The approach of comparing the data to a linearly damped sine wave is similar to a Gabor-Helstrom transform, in which the sine wave is damped by a Gaussian function; we chose to use a linear damping because it is less likely to yield spurious periodicities simply because the firing is bursty. A Fourier series analysis of these correlograms was not used because we use a finite time window, t, and a Fourier analysis assumes that the function repeats with a periodicity of t, and hence imposes a frequency resolution of $1/t$, which is ±5 Hz for a window of 200 ms.

OSCILLATION INDEX. An index was calculated to measure the oscillatory firing of a cell: the size of the central peak of the averaged autocorrelogram (half the distance from peak to trough) was measured and divided by the height of the averaged trial-shuffled autocorrelogram.

Histology

At the end of each experiment a lethal dose of sodium pentothal was given and the animal was perfused with saline followed by fixative (2.25% glutaraldehyde, 0.75% formaldehyde, 0.9% NaCl, 0.1 M sodium phosphate, pH 7.5). The cortex was frozen, cut in tangential sections 50 μm thick, and stained for cytochrome oxidase (Wong-Riley 1979). I used the small lesions made during recording to correlate the physiological observations with cytochrome-oxidase histology.

RESULTS

Oscillations in single cells

At least 10 responses to an optimal stimulus were recorded from each of 608 single units in 16 experiments in squirrel monkey V-1. In autocorrelograms calculated from these responses, one can see that the firing was often quite bursty and periodic. Figure 1 shows a 1-s recording from a single unit in layer 3 responding to an optimal white bar. For the first 200 ms of the response, the cell fired irregularly, but for the second half the spikes occurred in bursts. An autocorrelogram of this bursty period (indicated by the thick line on the spike record) indicates that the bursts occurred regularly, at 13-ms intervals. During the bursty firing of the single unit, the local field potential became larger and more regular. The local field potential is a lower frequency band signal recorded from the same electrode as the single unit, so it obviously reflects activity in that single unit, but it also reflects activity in other cells in the vicinity, heard as background hash in the high-frequency band spike recording.

The spike-triggered average of the local field potential shows oscillations correlated with the bursts in the single unit, indicating that other cells near the electrode tip were also firing in bursts, synchronously with the single unit. The most obvious artifactual explanation for the bursts would be that they were a response to the 60-Hz refresh rate of the TV monitor, but the right half of Fig. 1 shows that the periodicity is clearly not 60 Hz.

Figure 2 shows the same cell responding to the same stimulus moved more slowly across the receptive field, giving a longer response. An autocorrelogram for the early part of the bursty firing (*left*) indicates that the bursts occurred at a frequency of 72.1 Hz, and an autocorrelogram for the last part of the response (*top right*) shows bursts occurring at 77.6 Hz. The spike-triggered average of the local field potential below each autocorrelogram shows that other cells in the vicinity were synchronized to these two different rhythms. At the bottom of the figure is shown the autocorrelogram calculated for the entire response. This cell is quite typical in having episodes of distinctly different periodicity within a single response to a smoothly moving bar.

As discussed below, other groups have failed to see periodicities in their correlograms, and it may be because they analyzed spikes collected over much longer periods of times,

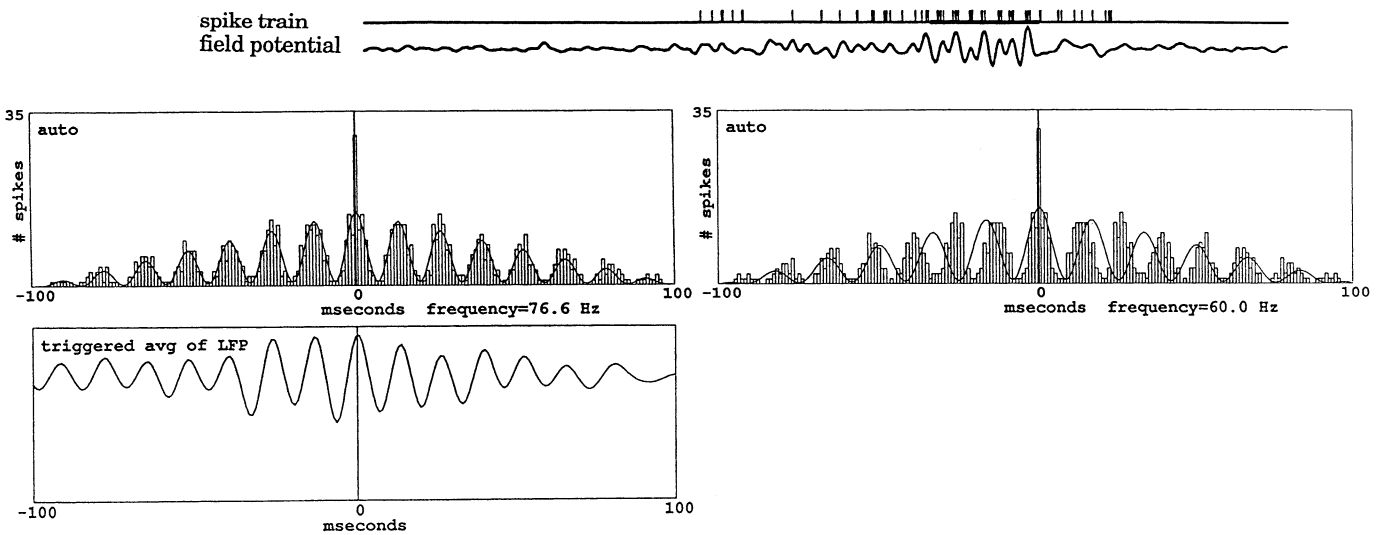

FIG. 1. Deep layer 3 cell responding to an optimal moving bar. *Top left*: autocorrelogram for this single trial, fitted with a 76.6 Hz damped sinusoid, for the period [interval T (T) = 100 ms] indicated by the dark baseline on the spike train. Time difference (t) = ±100 ms. *Bottom*: spike-triggered average of the local field potential. *Top right*: this correlogram is shown to fit poorly with a model having a modulation frequency of 60 Hz.

during which the oscillation frequency very probably varied. Indeed the autocorrelogram in Fig. 2 calculated for the entire 600-ms response (*bottom*) does not show as clear a rhythmicity as is apparent in the correlograms for shorter times. Therefore when looking at oscillations we usually calculated correlograms for short time periods (T = 100–500 ms, depending on the duration of the response). Because the comparison window (t) for these correlograms is often as long as the period being analyzed (T), and we do not count spikes outside of T, the correlograms have an overall triangular shape.

There were certainly many responses showing no periodicity and some that were borderline, but many responses were as obviously rhythmic as the ones illustrated here. To

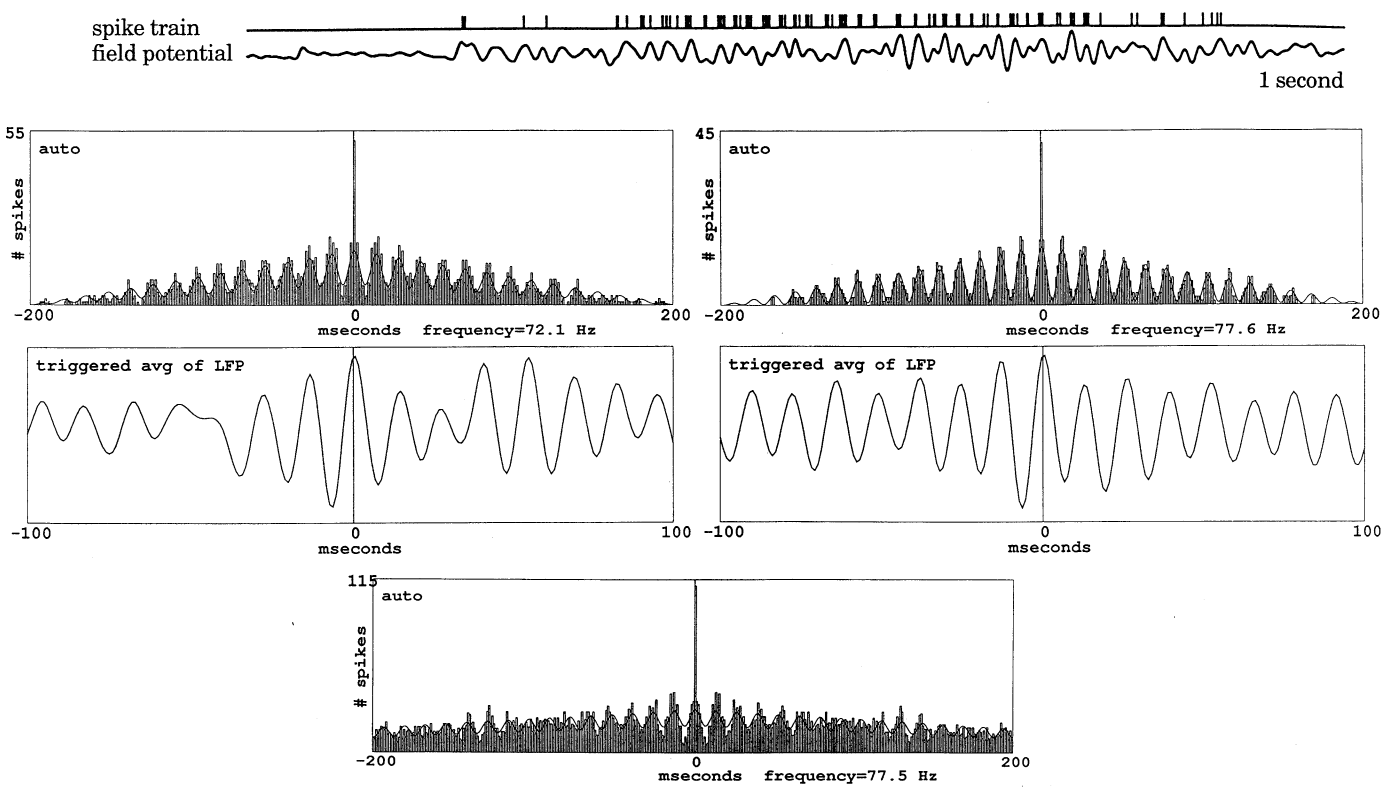

FIG. 2. One response of the same cell as in Fig. 1 to a slowly moving bar. The best fit of the model for each correlogram is shown. On the left are shown the autocorrelogram and the spike triggered average of the local field potential for the 1st 200 ms of the bursty part of this response (T = 400–600 ms). On the right are shown the autocorrelogram and the spike triggered average of the field potential for the 2nd 200 ms of the response (T = 600–800 ms). Below is shown the autocorrelogram for the entire response (T = 200–800 ms). t = ±200 ms.

TABLE 1. *Number of cells showing oscillatory firing in each cortical layer*

Cortical Layer	Cells Showing Oscillatory Firing in >25% of Responses
2/3 interblob	144/293 (49)
2/3 blob	2/3 (67)
4B	68/133 (51)
4Cα	8/35 (23)
4Cβ	0/13 (0)
5	4/23 (17)
6	8/40 (20)
Total	234/540 (43)

Number of cells assigned to each cortical layer showing oscillatory firing. Percentages are in parentheses. A cell was counted as showing oscillatory firing if at least 25% of the responses recorded qualified as being oscillatory. To determine if a response was oscillatory, a series of linearly damped cosine waves of frequencies between 30 and 100 Hz were multiplied times the autocorrelogram of the response itself. If the product of the best frequency and the response autocorrelogram was >4 SD larger than the average product for the rest of the frequencies tested (excluding ±10 Hz around the best frequency) then the response was counted as being oscillatory. Anecdotally, the cells in layer 2/3 that seemed to be most oscillatory were in the deeper parts of that layer.

get some idea of how common periodic firing was, we used a least-squares approximation to fit each correlogram with a model—a damped sinusoidal modulation of the average expected correlogram for theoretical train of the same number of spikes occurring randomly. A correlogram was counted as having significant oscillatory firing if the probability that correlogram could have arisen from a random spike train was <1% (see METHODS). All responses that gave a best fit to a modulation of 60 or 30 Hz were rejected. For all the cells studied, the range of oscillation frequency was from 40 to 80 Hz, with most of the cells firing with a periodicity ~50 Hz. Table 1 shows how often cells that could confidently be assigned to a particular layer showed oscillatory firing in at least *some* (25%) of their responses. In the upper layers, about half the cells in layer 2/3 and in layer 4B cells showed significant oscillatory firing during at least 25% of their responses. At first it seemed that the most oscillatory cells were in layer 4B, but in some experiments, oscillatory cells were histologically identified as being in layer 2/3; however, those cells were almost always in the deepest parts of that layer. A few cells showed strikingly periodic firing: 24 deep layer 2/3 cells and 8 layer 4B cells showed oscillations in >80% of their responses. A quarter of the cells recorded in layer 4Cα and none of the cells recorded in layer 4Cβ showed oscillatory firing in >25% of their responses. In the deep layers, about one-fifth of the cells showed periodic firing in >25% of the responses. Of three unoriented color-opponent blob cells, two showed oscillations in more than one-half of their responses.

These statistics probably underestimate the number of cells that fire periodically for two reasons. First, only cells giving vigorous responses showed significant oscillations in their correlograms, simply because any pattern in a small number of spikes was usually not statistically significant. Second, the local field potential usually showed regular waves during a visual response, even when the simultaneously recorded single unit did not show oscillatory firing.

Controls for artifactual oscillations

The first concern was to find out if the rhythmic firing observed was anything more than a response to the 60-Hz refresh rate of the TV monitor or to some jitteriness in the stimulus motion. This is especially important because magnocellular LGN cells can respond to flicker as fast as 60 Hz. But most of the oscillation rates were distinctly different from 30 or 60 Hz, and, as shown in Fig. 2, the oscillation rate varied from one response to the next, and even within a single response. Also we have used constant light sources. As shown in Fig. 3, this same cell also fired rhythmically in response to a tungsten light source. For most of the experiments in this study we used a liquid crystal projector, which also produces no 60-Hz flicker, and which can be driven by our Iris computer. With this projector as well, single cells exhibited oscillatory firing, and firing between cells was often correlated, as described later. This projector of course does not produce completely smooth moving stimuli, as it uses video technology to generate the image (60-Hz interlaced). Thus the bar moves by changing the color of pixels at its front or back edge, and this change is generated at 60 Hz. But any synchronization or rhythmic response to this kind of artifact should show up in the trial-shuffled correlograms (see below). Indeed a small fraction of the cells did show shuffled correlograms with sharp periodicities at exactly 60 Hz, and these cells were eliminated from the study.

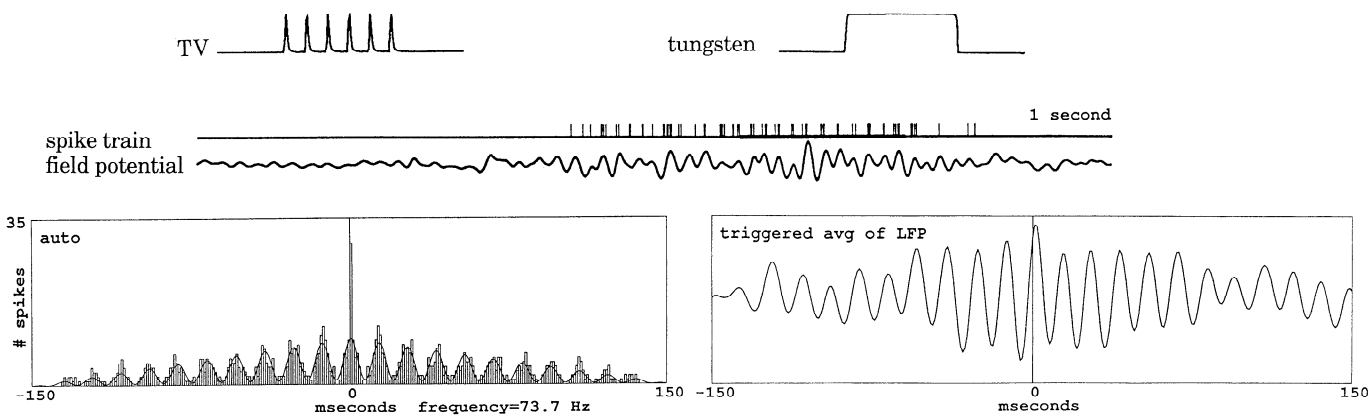

FIG. 3. *Top*: photocell responses to 100 ms pulses of light from the TV and tungsten light sources. *Middle*: a response of the same cell as in Figs. 1 and 2 to a stimulus generated by the tungsten source. *Bottom*: autocorrelogram and the spike triggered average of the field potential for this single response. T = 150 ms; $t = \pm 150$ ms.

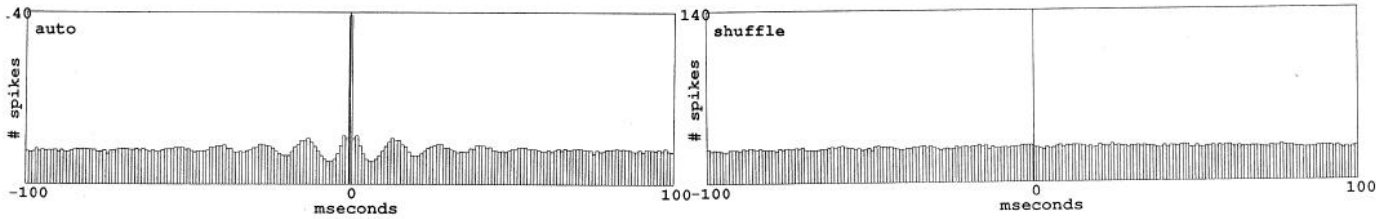

FIG. 4. Averaged autocorrelogram and trial shuffled correlogram for a series of 35 consecutive responses from the same cell as shown in Figs. 1–3. Response in Fig. 2 was one of these responses, but the time window used was 900 ms, and t was ±100 ms. Flat trial shuffled correlogram indicates that the responses were not phase locked to some aspect of the stimulus presentation.

Other things besides cortical connectivity, such as irregularities in the stimulus motion or receptive-field substructure, could produce artifactual regularities in the firing. I therefore calculated trial-shuffled correlograms to see if periodicities in the responses were time-locked to the visual stimulus. To obtain a trial-shuffled autocorrelogram, a correlogram was calculated between each response in a series and the subsequent response; these correlograms were averaged for the entire series. Figure 4 shows the average (not shuffled) autocorrelogram (*left*) for 35 consecutive responses, from the response series that gave the raw correlogram in Fig. 2. Twenty-one of the autocorrelograms in this series showed significant oscillations, as in Fig. 2, but the averaged autocorrelogram has smaller peaks because of the variation in burst frequency. On the right is the trial-shuffled correlogram for the same 35 responses. The shuffled correlogram is flat, indicating that the responses were not phase locked to some aspect of the stimulus, ruling out receptive-field substructure, stimulus flicker, or jittery stimulus motion as a source of periodicity. The same criterion for significance was applied to the shuffled correlograms, namely, the best fitting damped cosine wave was determined for the correlogram, and the correlogram was said to be oscillatory at that frequency if the product of the correlogram times the best fitting model was four standard deviations larger than the average of the products of the integral frequencies (30–90 Hz) times the correlogram. If the trial-shuffled correlogram of a cell was not flat (that is if it did show significant oscillations), it was rejected. A few cells did show oscillatory shuffled correlograms, though almost invariably at 30 or 60 Hz and therefore probably related to the redraw rate of the computer; they were eliminated from the study.

For this trial-shuffling calculation to be valid the data collection must be precisely synchronized to the stimulus generation. Therefore, to test this, we put a photocell on the monitor and moved a thin bar rapidly across it for 30 trials, recording 1 "spike" per trial. The resulting shuffled correlogram shown in Fig. 5 indicates that our data collection is indeed precisely synchronized to the stimulus, as the single "spike" in each trial occurs in the same time bin as the "spike" in each other trial.

I calculated autocorrelograms for single responses of only 100–500 ms duration, which is an unconventionally short time, but in auto-correlograms averaged over many responses, the periodicities in the firing were usually not nearly as evident.

Correlations between the firing of different cells—different depths in the same layer

Because the local field potential recordings had indicated that many cells in a local area could participate in these oscillations, I wanted to see if they occurred throughout the depth of the cortex, and in particular whether correlations occurred between the different functional streams. In five experiments I made penetrations perpendicular to the pial surface with pairs of electrodes glued together side by side with the tip of one electrode 300–500 μm longer than the other (Fig. 6). The first or reference electrode in these correlograms is arbitrarily

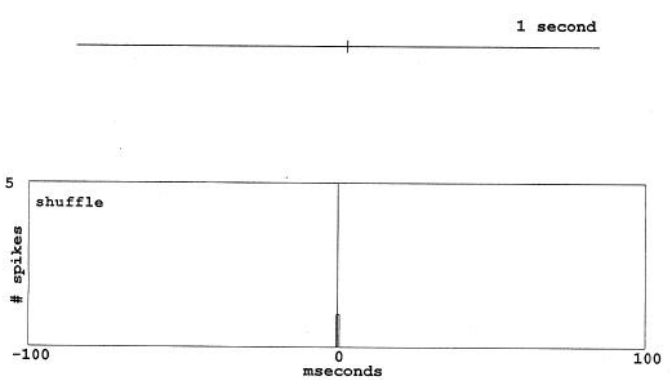

FIG. 5. Test for synchronization of stimulus generation and data collection. A photocell was placed on the front of the TV monitor, and a 1-pixel wide bar was swept rapidly across the screen. A trial shuffled correlogram for 30 responses of the photocell fill only the 0-ms bin, verifying the synchronization of the data collection and stimulus generation.

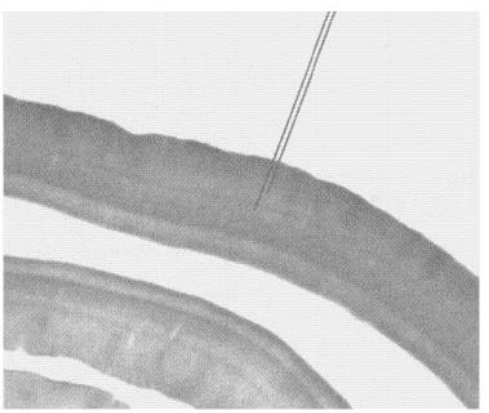

FIG. 6. Diagram showing how pairs of electrodes, used in the experiments shown in Figs. 7–9, would 1st penetrate striate cortex on the outer convexity of the occipital lobe, and then would penetrate the underlying roof of the calcarine fissure, crossing through the layers in reverse order, from deep to superficial.

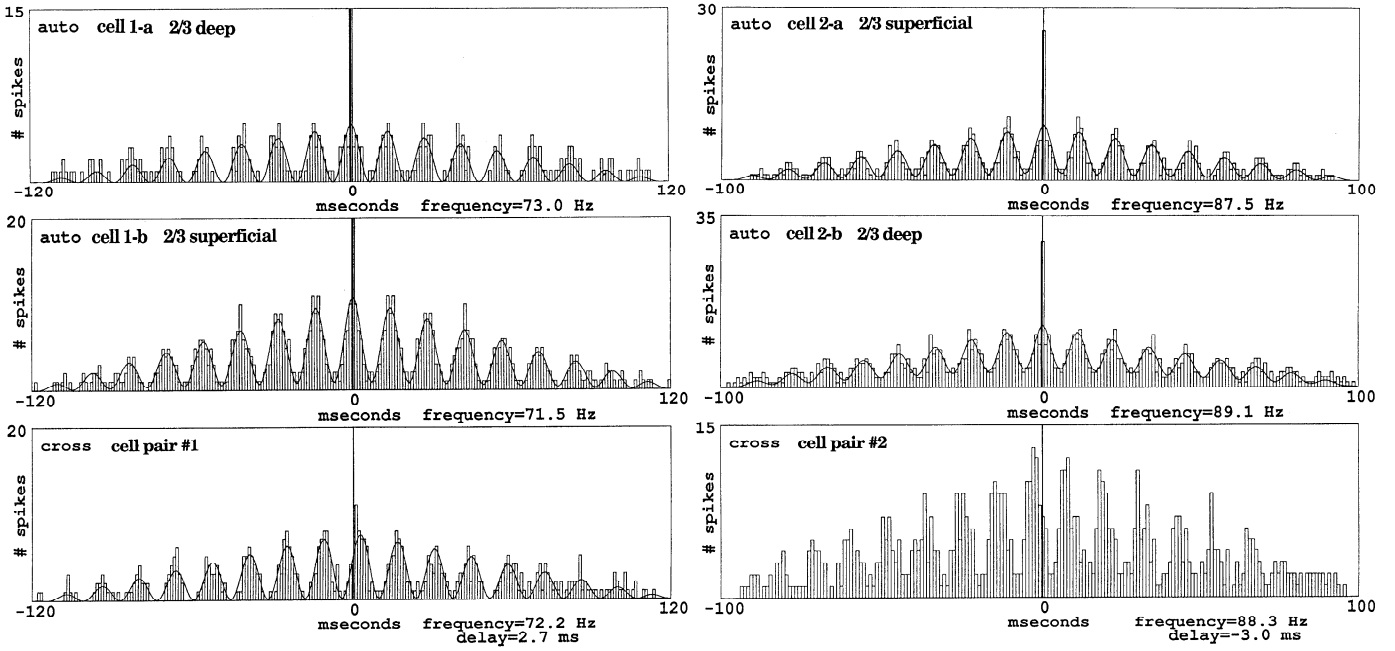

FIG. 7. Two sets of correlograms from single responses in an experiment with the 1st electrode 300 μm longer than the 2nd. First set (*left*) was taken early in the experiment when the monkey was anesthetized with halothane. T = 120 m; $t = \pm 120$ ms. Electrodes were in the upper fold of cortex—1st electrode in deep layer 3, the 2nd 300-μm above in superficial layer 2/3. Both cells had exactly the same orientation selectivity, and were stimulated by a single bar. *Top* and *middle*: autocorrelograms; oscillatory firing for both cells strongly indicated. Cross-correlogram (*bottom*) is also periodic, reflecting the fact that both cells oscillated at the same frequency, but the offset of the peak indicates that the bursts in the superficial cell tended to occur ~3 ms after each burst in the deeper cell. Responses on the *right* were recorded many hours later in this same experiment. T = 100 ms; $t = \pm 100$ ms. Electrodes had crossed the calcarine sulcus and entered the fold of V-1 below. Again both autocorrelograms show periodic firing, and the cross correlogram shows that the cell in the 1st electrode, which was now in a more superficial part of layer 2/3 tended to fire, on average, 3-ms after the cell recorded by the 2nd electrode, which was in deeper layer 2/3. That is, in both folds of cortex, the cross-correlograms indicate that spikes in deep 2/3 tended to precede those in superficial 2/3. Several hours earlier I had switched the anesthetic from halothane to sufentanil. (I saw similar oscillatory firing under nitrous oxide anesthesia as well.)

always the longer electrode, so in the first thickness of cortex the first electrode is deep to the second; however, the laminar positions are reversed after the electrodes pass through the first thickness of cortex and into buried cortex. Figure 7 shows two sets of correlograms from single responses in an experiment in which the first electrode was 300 μm longer than the other. The spikes for the first set of correlograms, shown on the left, were recorded early in the experiment. The electrodes were in the upper fold of cortex—the first electrode in deep layer 3, and the second 300 μm above in superficial layer 2/3. Both cells had exactly the same orientation selectivity, and could be stimulated by a single bar. All the records were made by using a single moving white bar, of optimal orientation and speed. The two upper records are autocorrelograms and indicate that both cells fired in regular bursts; that is, they were both strongly oscillatory. The cross-correlogram (*bottom*) is also periodic, reflecting the fact that both cells oscillated at the same frequency, but the central peak of the cross-correlogram is not centered at zero, but rather occurs at +2.7 ms. This offset of the peak indicates that the bursts in the superficial cell tended to occur ~3 ms after each burst in the deeper cell. The responses from which the correlograms on the right were calculated were recorded many hours later in this same experiment. The electrodes had crossed through white matter to the cortex of the roof of the calcarine sulcus, so the first electrode was then closer to the pial surface than the second electrode. Again, the autocorrelograms show that both cells exhibited regular bursty firing, and the −3 ms offset in the cross-correlogram indicates that spikes in the deep cell (now the 2nd electrode) again preceded those in the superficial cell.

Figure 8 shows the averaged correlograms for 30 consecutive responses for the pair of cells shown on the left side of Fig. 7. Even though most individual responses were just as bursty as those shown in Fig. 7, in the averaged autocorrelograms the peaks are smeared out by the variation in frequency and timing of the bursts. The offset of the peak in the cross-correlogram indicates that throughout this series the superficial cell tended to fire ~3 ms after the deep cell. Again, to test for some stimulus-driven source for the correlation, I calculated a trial-shuffled cross-correlogram, shown on the bottom, which is flat, indicating that neither the correlations between the cells nor the oscillatory firing were stimulus locked. Recordings from 15 such pairs of vertically aligned cells, both in layer 2/3 but with one electrode 300 to 500 μm deeper than the other, all gave similar results: spikes in the cell in deep layer 3 preceded spikes in the cell in superficial 2/3 by an average of 3.1 ms (SD = 1.6 ms).

A correlogram with a single peak at a delay of 3 ms could be interpreted as showing that the second (deep) cell had a direct synaptic input to the first (Bryant et al. 1972; Palm et al. 1988). Indeed, anatomic studies indicate that thalamic input layer 4Cβ projects to the deep half of layer 3 but not to the more superficial part, and that cells in deep layer 3 send axons to more superficial layer 2/3 (Fitzpatrick et al. 1985; Lund and Boothe 1975). This would be consistent with a flow of information from layer 4 to deep 3 and then

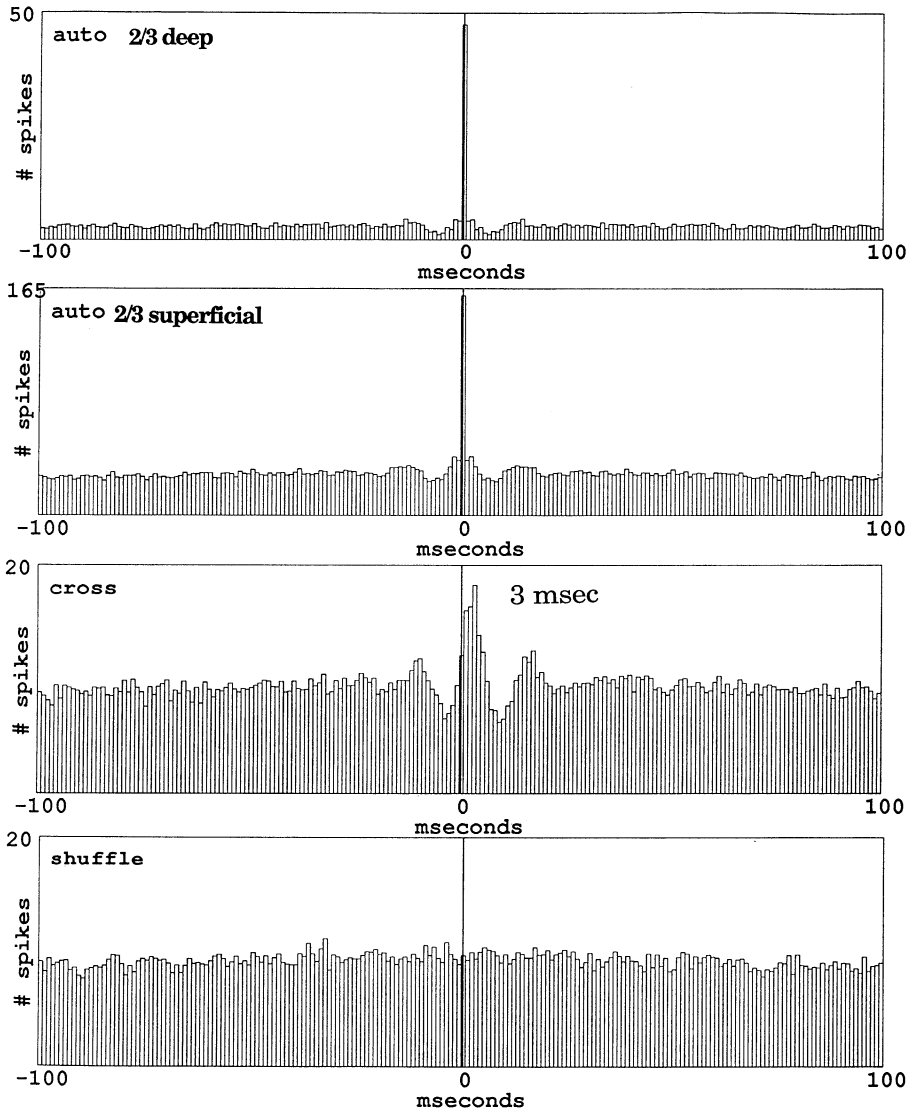

FIG. 8. Averaged correlograms for 30 consecutive responses for the pair of cells whose responses are shown in on the left in Fig. 7. T = 900 ms; $t = \pm 100$ ms. Flat trial shuffled correlogram indicates that the correlations in firing patterns seen in the cross-correlogram are not the result of some stimulus-dependent firing patterns or the receptive-field substructure.

to more superficial 2/3. But the oscillatory firing of both cells suggests a more complicated interaction, and there are indeed multiple potential sources for feedback from superficial 2/3 to deep 2/3 (for review see Lund 1988).

Different layers in the same column

Because of the laminar segregation of magno and parvo streams in V-1, cells in different streams can lie directly above and below each other within the same cortical column, so I was particularly interested to learn if cells in the same column but in different layers would show correlated firing. Layer 4B receives its input from the magnocellular geniculate layers via layer 4Cα. Layer 4Cβ receives exclusively parvocellular input and anatomically provides most of the input to layer 2/3, though there is anatomic and physiological evidence for some magnocellular influence in layer 2/3 (Blasdel et al. 1985; Hubel and Livingstone 1990; Hubel and Wiesel 1972; Lund 1973; Lund and Boothe 1975; Nealey and Maunsell 1994). When the deeper electrode passed into layer 4B, the cells' firing continued to be correlated with that of cells in layer 2/3 directly above, with the spikes in 4B preceding the layer 2/3 cell by 3 or 4 ms (Fig. 9).

In 10 pairs of vertically separated cells, with one in layer 2/3 and the other 300–500 μm directly below in 4B, the average delay was 2.9 ms (SD = 1.4 ms). The delay between two equally distant cells, both within 2/3, is also ~3 ms, and hence there seems to be no extra delay between layer 4B and 2/3. The synchrony between layers 3 and 4B in any case provides evidence for crosstalk between the two major streams, magno- and parvocellular. There was no significant further time shift as the electrode passed into layer 4Cα, but not enough cells have been recorded in that layer to be certain. Of the few cells recorded in layer 4Cβ, none showed oscillations, and their firing did not seem to correlate with cells in other layers. This is surprising because that layer provides input to layer 2/3, so one would expect at least to see a peak in the cross-correlogram between a cell in layer 2/3 and one in layer 4Cβ consistent with monosynaptic input. The inability to record any correlations between layer 4Cβ and layer 2/3, despite the finding of correlations between cells within layer 2/3, suggests that monosynaptic inputs are not the only way to produce correlated firing.

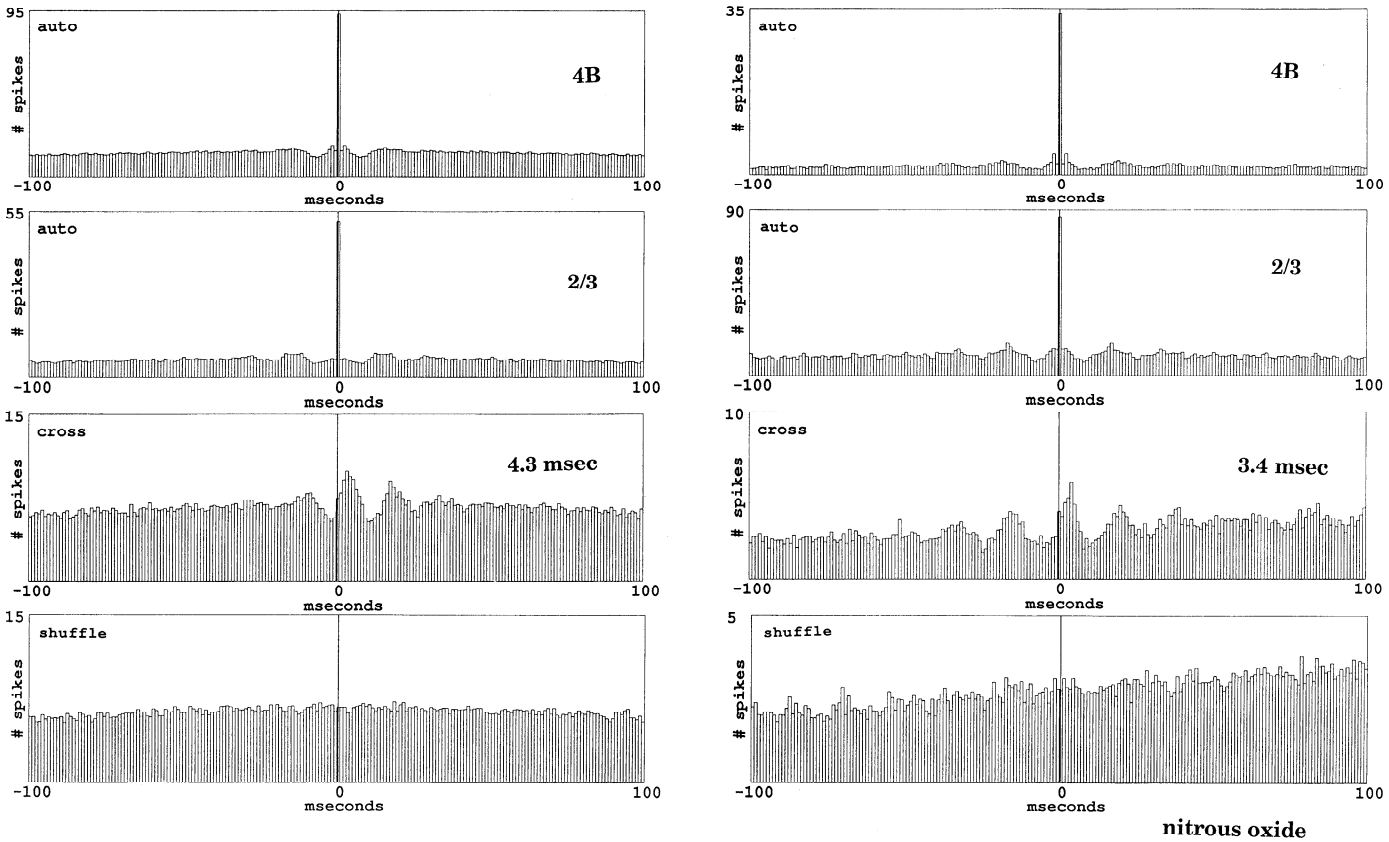

FIG. 9. Averaged cross-correlograms for 78 (*left*) and 44 (*right*) responses from 2 different pairs of cells in 4B and deep layer 3. In the *left example* the 1st electrode was in layer 4B and the 2nd 400-m above in 2/3. For the *right example,* the electrodes had crossed the calcarine sulcus, and the 1st electrode was in layer 2/3 and the 2nd electrode in 4B. Both averaged cross-correlograms indicate that the spikes in 4B preceded those in 2/3 by a few milliseconds on average. Trial-shuffled correlograms are flat, indicating that the peaks in the cross-correlograms reflect neuronal interactions rather than stimulus-driven correlations. For both sets of records T = 850 ms; $t = \pm 100$

Correlations between the upper layers and layers 4Cα or 4B are consistent either with magno/parvo synchronization or with a magnocellular contribution to the upper layers.

Same layer; different columns

These results so far indicated that cells within a single orientation column tended to be correlated, and I wanted to look at cells horizontally separated, and therefore in different columns. One of the most intriguing results from Gray and Singer's work in the cat is that cells with nonoverlapping receptive fields exhibit synchrony most often when they have the same orientation selectivity and are stimulated by a single contour. To see if this was true in the monkey, I made penetrations with three or four parallel electrodes.

Ts'o and Gilbert (1988) had previously found that nearby cells in monkey visual cortex show correlated firing only if they have similar receptive field properties, but they did not ask whether a single stimulus activating both cells produced stronger correlations than independent stimuli. I began by making vertical penetrations in V-1 by using sets of 3 or 4 parallel electrodes spaced 1–2 mm apart, so that the tips would be in the same layer but in different columns. Figure 10 shows 3 responses, and their correlograms, from a series of 25 consecutive responses, from a pair of cells 1 mm apart in layer 2/3. Figure 11 shows the averaged correlograms for all 25 responses. The two cells had similar orientation selectivity, and the receptive fields were close enough that it was possible to activate both of them simultaneously with a single bar. Averaging many correlograms increases the sensitivity for detecting temporal relationships between cells, but it forfeits information about oscillation frequency in each cell, because all but the central peaks are averaged out by the variation in frequency, as can be seen by comparing the single-response correlograms in Fig. 10 and the averaged correlogram in Fig. 11.

Figure 12 shows correlograms for another pair of cells, 1.8 mm apart, both in deep layer 3 with orthogonal orientation preferences. The left set of correlograms was calculated from a response to a moving bar oriented optimally for the upper cell (and to which the second cell gave very little response), and the right set of correlograms was calculated from a response to a bar to which the lower cell, but not the first cell, responded well.

Figure 13 shows averaged correlograms for 30 responses from 2 other pairs of cells 1 mm apart. The pair of cells shown on the left had the same orientation selectivity, and the pair on the right had orientation selectivities that differed by 55°. The auto-correlograms indicate about the same degree of periodicity in firing for both pairs of cells, but the cross-correlograms indicate more synchrony for the pair of cells with similar orientation preferences stimulated by a single bar.

To quantify the degree of synchrony between two cells,

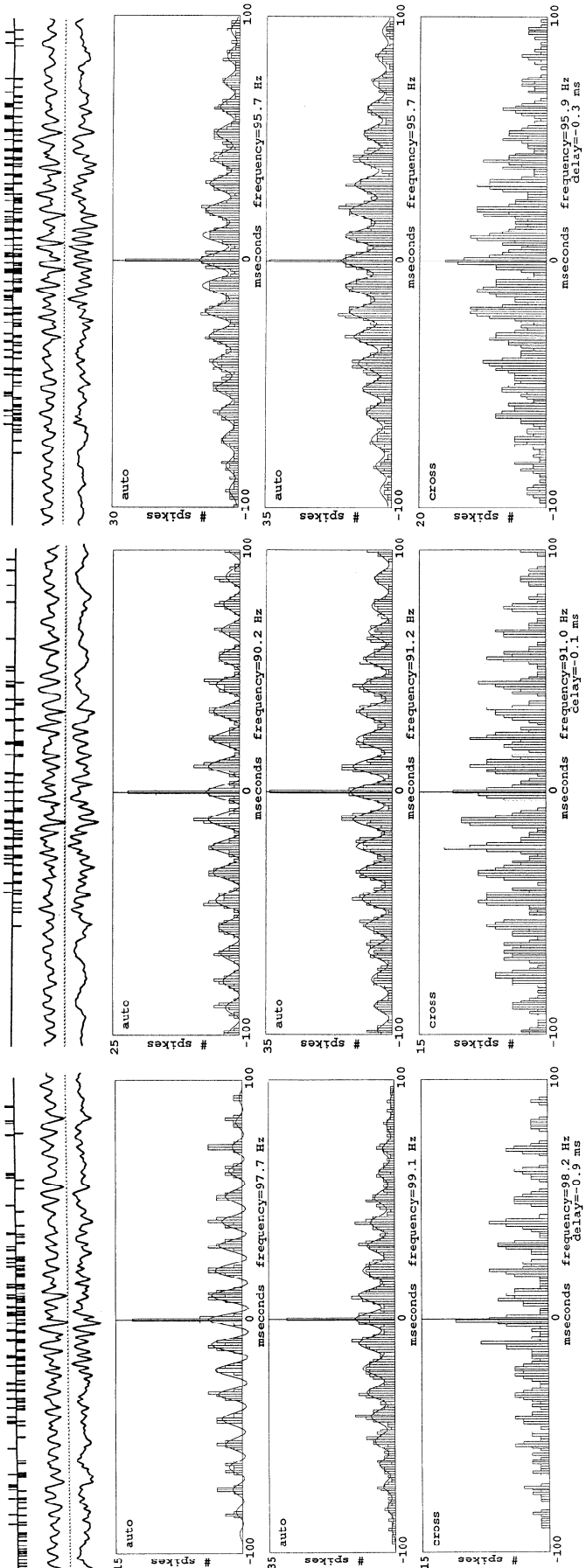

FIG. 10. Correlograms for 3 single responses for 1 pair of cells in different columns, stimulated with a single optimal bar. These 2 cells were ~1 mm apart (horizontally across the cortex) and had similar orientation preferences. They were both in deep layer 2/3. In each response selected, both cells showed oscillatory firing and the frequency was very similar for the 2 cells. Each cross-correlogram peaks at 0 ms, indicating that the bursts in the 2 cells were synchronized. The synchrony between the cells can be seen in the spike trains and in the field potentials. For the 1st set of records, T = 100 and t = 100 ms; for the 2nd set, T = 140 and t = 100 ms; for the 3rd set, T = 100 and t = 125 ms.

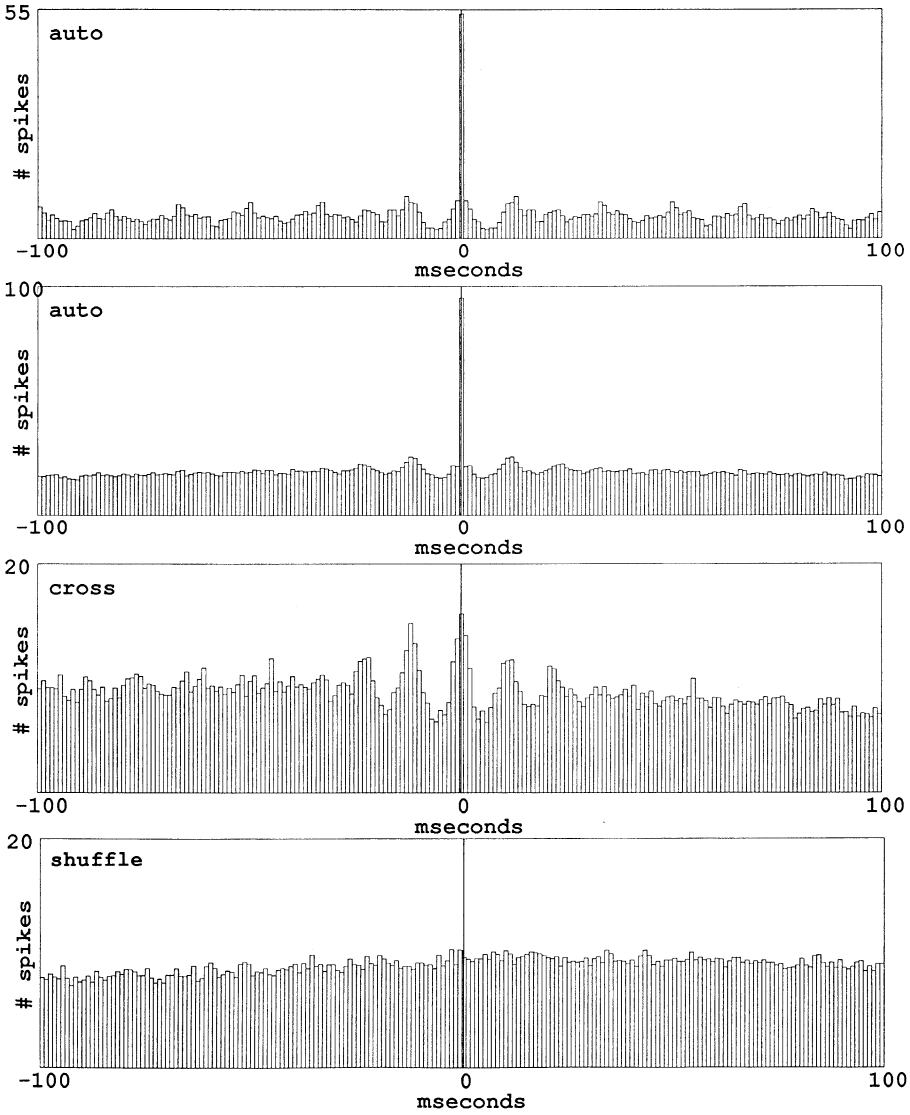

FIG. 11. Averaged cross-correlogram (*left*) and trial-shuffled correlogram (*right*) for 25 consecutive responses, including those shown in Fig. 10, for the 2 cells in Fig. 10, stimulated with a single bar. Cross correlogram shows that the cells tended to fire simultaneously and rhythmically, and the flat-shuffled correlogram indicates that the correlations were not stimulus driven. T = 900 ms; $t = \pm 100$ ms.

I measured the height of the central peak (half the distance from trough to peak) of the averaged cross-correlogram and divided it by the baseline correlation, which is the height of the averaged trial-shuffled correlogram, and called this the *correlation index* (see Fig. 13). This index reflects the fraction of spikes that are correlated, beyond what would be expected from two randomly related spike trains. Figure 14 summarizes these results, for all the pairs of cells recorded that were 1–2 mm apart on the cortex. Each point indicates the correlation index calculated from averaged cross- and shuffled correlograms, each pair averaged across at least 20 trials. Interneuronal synchrony was not significantly stronger between cells of similar orientation selectivity than between cells of different orientation selectivity. For cells with close to the same orientation selectivity the correlation was stronger if both cells were stimulated by a single bar of intermediate orientation than by two optimal bars ($P < 0.05$, paired t-test). If the receptive fields of two cells were separate enough that they could be activated independently, the cells tended to show stronger correlations to a single bar than to two bars moving in opposite directions ($P < 0.05$, paired t-test).

Figure 15 shows that in some experiments, a pair of cells 5 mm apart, with similar orientation selectivity, also can show correlated firing. These two cells had receptive fields separated by 1°, and the two fields were displaced from one another along the axis of their preferred orientation, so the two cells could be stimulated either by different bars or by a single long bar. When these two cells were stimulated by a single long bar they both showed regular bursty firing, as indicated by the auto-correlograms, and their firing tended to be synchronous, as indicated by the peak centered at zero in the cross-correlogram. When they were stimulated by two short bars moving in opposite directions, both cells also showed oscillatory firing, but the cross-correlogram indicates that their firing was slightly less synchronized than when they were stimulated by a single bar. The heights of the 0-ms bins in the auto-correlograms are about the same, indicating that the response, the absolute firing rate, was similar for the two conditions, and thus a stronger response to one or the other stimulus cannot explain the difference in degree of synchrony.

For this same pair of cells, I also recorded 30 epochs of spontaneous activity, with no visual stimulation, and the

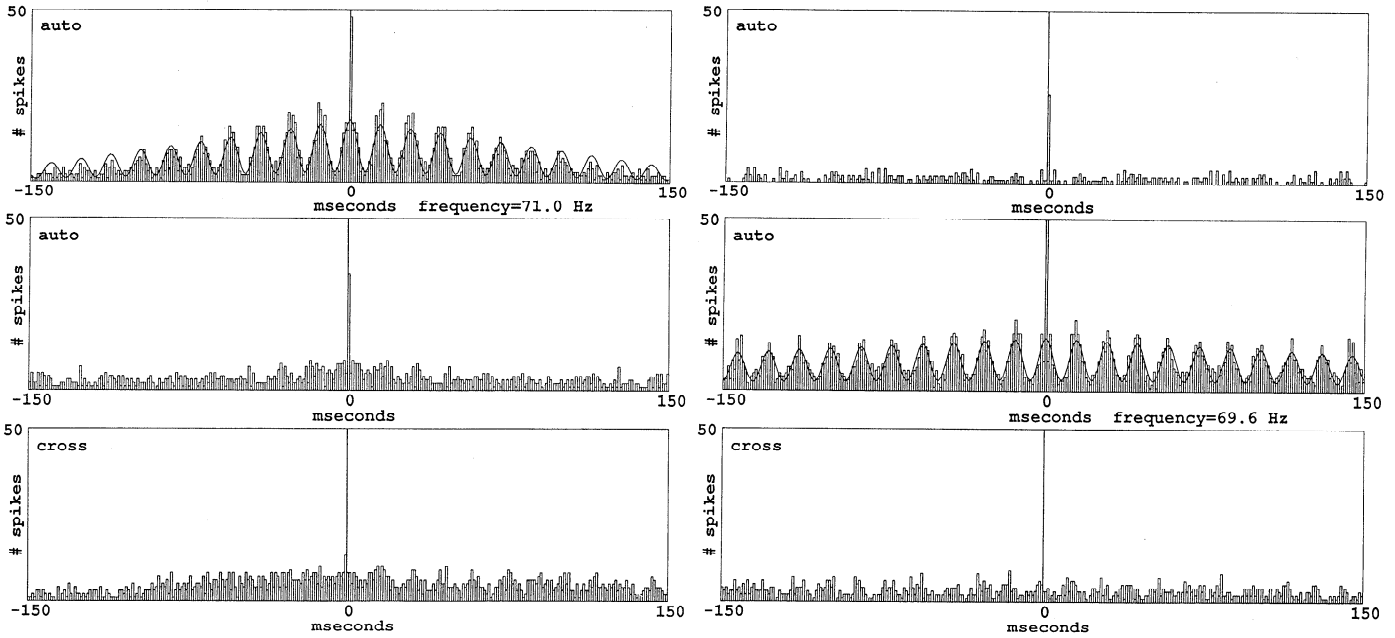

FIG. 12. Auto- and cross-correlograms for 2 single responses from 1 cells 1.8 mm apart, both in deep layer 3, with orthogonal orientation preferences. Left set of correlograms was calculated from a response to a moving bar oriented optimally for the upper cell, and the right set of correlograms was calculated from a response to a moving bar oriented optimally for the lower cell. Because the 2 stimuli were presented at different speeds, the responses were of different durations, and correlations were calculated over different time windows; for the left set, T = 200 ms and $t = \pm 150$ ms; for the right set, T = 500 ms and $t = \pm 150$ ms.

correlograms calculated from those spontaneous spikes are shown in Fig. 16. These two cells are typical of all the cells studied in that in the absence of visual stimulation the auto-correlograms are flat, indicating that there is no rhythmicity to their spontaneous activity, and the cross-correlograms show no evidence for synchrony.

Figure 17 summarizes the behavior of all the cell pairs recorded that were separated by 2–5 mm. On average, cells with similar orientation selectivity, stimulated with a single bar, showed more synchrony than cells with different orientation preferences ($P < 0.05$, unpaired t-test), but this difference is at least partly the result of the difference between being stimulated with one bar versus two—the difference between the average correlation index of cells of different orientation selectivity (stimulated with 2 bars) and the average correlation index of cells of the same orientation selectivity also stimulated with two bars was only marginally significant ($P = 0.056$), and cells of similar orientation selectivity showed stronger synchrony when stimulated with one long bar (or 2 parallel bars moving in the same direction) than with two bars moving in opposite directions ($P < 0.05$, paired t-test). Synchrony between cells of different orientations was significantly less for cells <2 mm apart, compared with cells >2 mm apart ($P < 0.05$, 1-tailed t-test), but there was no significant difference in the degree of synchrony between cells of similar orientations at the two cortical distances. These results are very similar to results in V-1 of the cat (Engel et al. 1990): cells with nonoverlapping receptive fields showed stronger interneuronal synchronization if they had similar orientation selectivity, but for cells with overlapping receptive fields, the degree of synchrony did not depend on whether the orientation selectivity was the same.

Is it the oscillations or the correlations that are important, or are they related?

The finding that interneuronal correlation, i.e., spike-by-spike synchrony, is usually stronger when two cells are stimulated by a single bar tends to support the hypothesis that correlated firing plays a role in linking related neuronal responses. Gray and his colleagues (1989) and Eckhorn et al. (1988) had emphasized that in the cat the correlated firing patterns are bursty and periodic. Computer-vision models that use temporal correlations for linking related responses often use reverberating feedback as a "mechanism for producing synchronization" (Johannesema et al. 1986; Koch et al. 1989; Sejnowski 1986; Sporns et al. 1989, 1991; von der Malsburg and Schneider 1986). The failure of some groups to find oscillatory firing in monkey visual cortex (Krüger and Mayer 1990; Young et al. 1991) has incited a controversy over whether oscillatory firing is unique to the cat and what its relationship is to interneuronal synchrony. As described above, I do find clear periodic firing in squirrel monkey striate neurons, and the observed short duration of the bursty periods and the variability in frequency easily explain why others might not have seen it. Some recent abstracts have described oscillatory firing in V1 of alert macaques (Eckhorn et al. 1995; Friedman-Hill et al. 1995; Gray et al. 1995), and Kreiter and Singer (1992) earlier reported oscillatory firing in macaque prestriate cortex.

It seemed that I saw the strongest interneuronal synchrony when both cells of a pair were bursty. This bursty firing was not the kind of firing characteristic of injured cells as it was exclusively driven by visual stimuli. Moreover, many cells were recorded for several hours, and showed the same kind of bursty firing over the entire time. Because the degree of interneuronal correlation seemed to be related to the degree

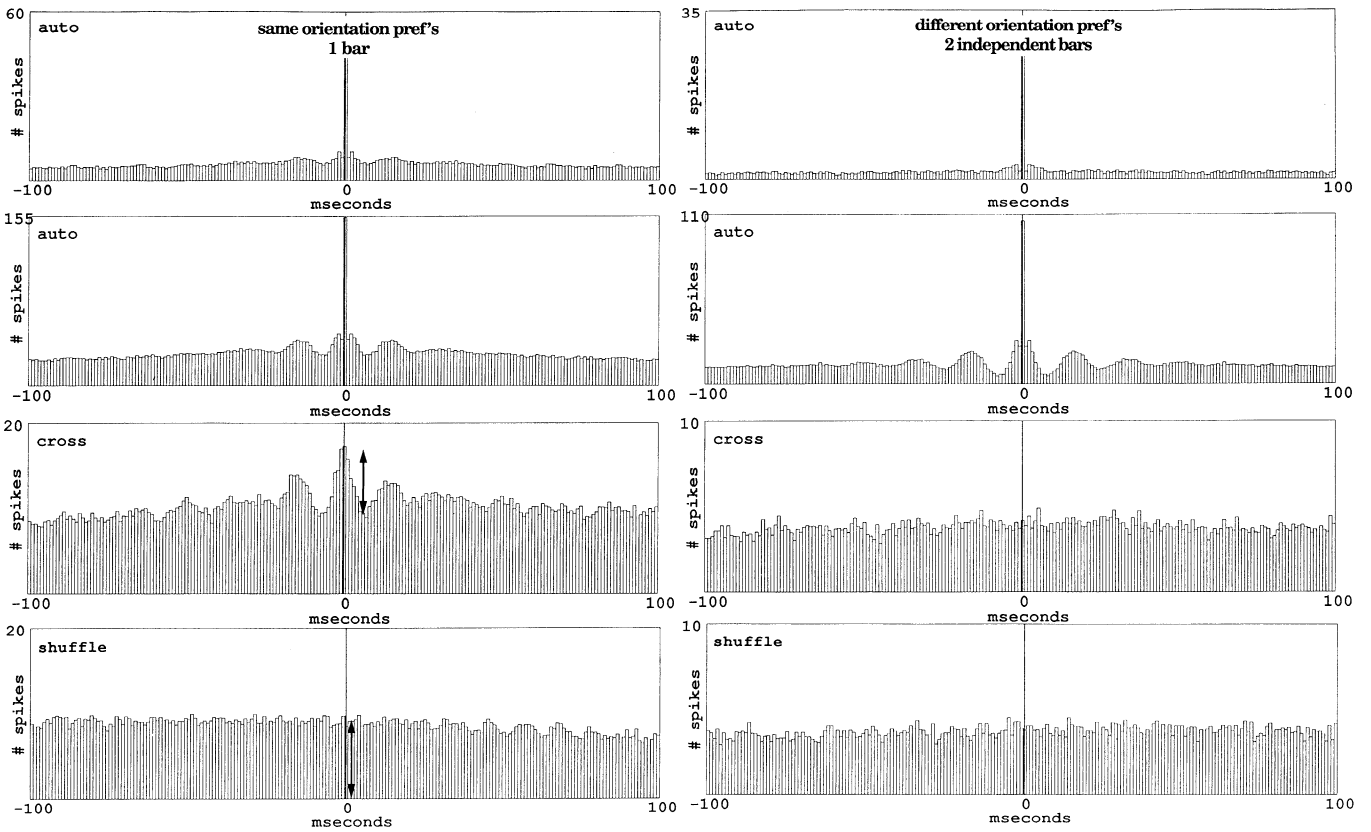

FIG. 13. *Left*: averaged correlograms for 32 responses from another pair of cells, both in 4B, 1 mm apart with similar orientation selectivity, stimulated with a single bar. Again there is a peak at 0 in the cross correlogram and a flat trial shuffled correlogram. *Right*: averaged correlograms for 29 responses from a pair of cells 1 mm apart in layer 2/3 with orientation preferences differing by 55°, stimulated by 2 optimal overlapping bars. Arrows on the cross- and shuffled-correlograms on the left indicate the measurements used to calculate a correlation index—half the peak-to-trough distance, divided by the height of the shuffled correlogram. Autocorrelograms indicate about the same degree of oscillatory firing for these cells as for the cells on the left, but the cross-correlogram indicates much less synchrony for the cells stimulated with 2 separate bars (correlation index for the 1st pair of cells = 0.41; correlation index for the right pair = 0.03). For both sets of records T = 900 ms, and $t = \pm 100$ ms.

of oscillatory firing, I asked whether in a series of responses the strength of oscillations in two cells covaried with synchronization between the two. I also asked whether the oscillation frequencies of the two cells covaried as it does, for example, in the three responses shown in Fig. 10, and if the covariance depended on the stimulus.

In 17 pairs of cells in which both cells showed frequent oscillatory firing, for a series of individual responses I compared the degree of periodicity in the firing and the correlation index between the two cells (METHODS, OSCILLATION INDEX and CORRELATION INDEX). Results from one such cell pair with similar orientation selectivities are shown in Fig. 18; for this pair the correlation coefficient between these two measurements was larger when the two cells were stimulated by a single long bar than when they were stimulated by two oppositely moving bars, but it was positive for both. The average correlation coefficient between burstiness and interneuronal synchrony was 0.67 for cells with similar orientation preferences stimulated by a single bar, indicating a fairly strong correlation between interneuronal synchrony and burstiness. The correlation coefficient was 0.44 for the same cells stimulated by two oppositely moving bars, and was 0.24 for cells with orthogonal orientation preferences stimulated by two independent bars. Thus for all stimulus conditions examined, the degree of interneuronal synchrony covaries with the degree of burstiness of the two cells. It could be argued that some external variable, such anesthetic level, influenced both the degree of synchrony and burstiness in general, but then the degrees of burstiness of both cells in each pair should covary, and they did not.

To ask whether the oscillation frequencies in the two cells were related, auto-correlograms were calculated for each 300-ms epoch of each response, and a frequency spectrum calculated for each epoch (see METHODS). If the largest peak in the spectrum between 30 and 90 Hz was >4 standard deviations larger than the average power in the spectrum, it was tabulated. The relationship between the frequency of the firing periodicity for these same two cells is shown in Fig. 19. Each symbol on the graph plots the oscillation frequency of one cell against the oscillation frequency of the other cell, for a single response to a swept bar. Filled diamonds represent responses to a single bar that stimulates both cells, and open circles represent responses to two bars moving in opposite directions. The correlation coefficient between the burst frequency in the two cells was 0.42 (and was significantly greater than zero; $P < 0.001$), indicating that the frequencies in the two cells covaried over different responses. The correlation coefficient between the frequencies in the two cells when they were stimulated independently was 0.14 (and was not significantly greater than zero).

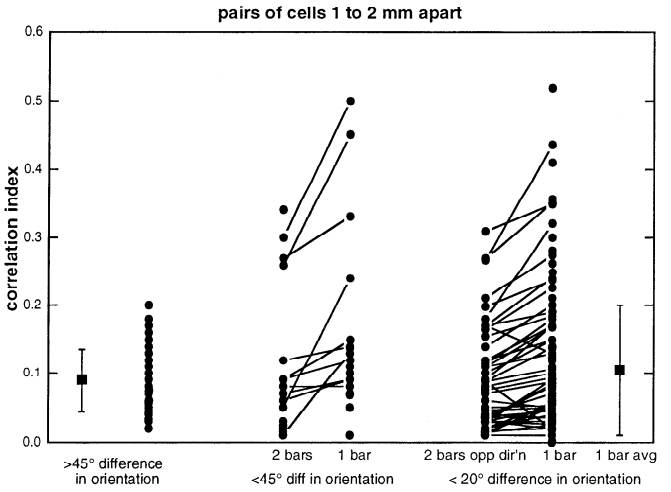

FIG. 14. Correlation index for 373 cell pairs recorded between 1 and 2 mm apart, calculated from averaged correlograms from at least 20 responses each. First set of symbols shows the correlation index for pairs of cells with optimal orientation selectivities that differed by more than 45°: filled circle, indices for each pair of cells; filled square at the far left indicates mean + SD. Middle set of symbols shows correlation indices for pairs of cells whose orientation preferences differed by 20–45° when the cells were stimulated by 2 separate bars optimally oriented for each cell or by 1 bar of an intermediate orientation. Lines connect correlation indices for the same pair of cells stimulated under both conditions; the correlation index for cells stimulated by a single bar is significantly larger than for the same cells stimulated by 2 bars ($P < 0.05$, paired t-test). Right sets of filled circles show correlation indices for pairs of cells whose orientation preferences differed by <20°. These cells were stimulated either with a single long bar that covered both receptive fields or (if the receptive fields were separate enough that the cells could be stimulated independently) by 2 parallel bars moving in opposite directions. Lines connect indices for each pair of cells stimulated under the 2 conditions; correlation index was significantly stronger for cells stimulated by a single bar than for the same cells stimulated by bars moving in opposite directions ($P < 0.05$). Rightmost square shows the average correlation index (± SD) for all cell pairs with orientation differences of 45°, stimulated by a single bar. Average correlation indices for cells with similar or different orientation preferences did not differ significantly.

I looked at 16 pairs of neurons >1 mm apart in which bursty firing was prominent enough in both cells to measure an oscillation frequency for >15 responses. Both cells in each pair had similar orientation preferences. The oscillation frequencies for the two cells were compared only for epochs during which both cells showed significantly periodic firing. For all 16 cells, the correlation coefficient (between the frequencies of oscillation for a pair of cells) for single bar stimulation was significantly above zero ($P < 0.001$), and was not for the two bar stimulation or for cells with different orientation preferences. The fact that the correlation coefficient is >0 for the single bar stimulation condition but is not when two bars were used suggests that the correlated oscillation frequencies in response to single contours do not simply reflect some global cortical rhythmicity but in some way must reflect the coherency of the stimulus.

Effects of anesthesia

Because anesthetics do induce slow waves in the EEG, it is important to find out if the periodicities in firing reported here resulted from the anesthetic. I tried several different anesthetics: halothane, nitrous oxide, and sufentanil, and found similar periodic firing and interneuronal synchrony with all three. For example, for the experiment shown in Fig. 6, the monkey was anesthetized with halothane for the first few hours of the experiment, when the cells shown on the left were recorded. Several hours later, the anesthetic was switched from halothane to sufentanil, and 2 h after that, the cells shown on the right of Fig. 6 were recorded. I saw similar oscillatory firing under nitrous oxide anesthesia as well (Fig. 9). In one experiment in which four electrodes were used, the animal was maintained for 5 h on halothane anesthesia. After that time, an additional 15 mg/kg ketamine was injected during recording from four single units, all of which had shown oscillatory firing and interneuronal synchrony. For the next 30 min after the injection of the ketamine there were only slight changes in the degree of periodic firing and interneuronal synchronization before the injection. (The 4 cells showed oscillatory firing in 43, 55, 46, and 46% of 121 spike trains before the ketamine injection, and afterward they showed oscillatory firing in 53, 54, 52, and 39% of the spike trains.) Thus whatever effects anesthetics have on patterns of firing, these effects are probably the same for different anesthetics.

DISCUSSION

The results described here indicate that, as in the cat, cells in monkey primary visual cortex often fire in synchrony, and often fire in periodic patterns. I find that pairs of cells, even when separated by up to 5 mm distance, can show correlated firing, often with zero phase lag. Several recent abstracts have also described both oscillatory firing and interneuronal synchronization in V1 of alert macaques (Eckhorn et al. 1995; Friedman-Hill et al. 1995; Gray et al. 1995). Kreiter and Singer (1992) earlier showed that cells in prestriate cortex of alert macaque monkey can show oscillatory firing and interneuronal correlations with zero phase lag. It is perhaps interesting that in this study I find that the strongest oscillatory firing occurs in layer 4B or deep 3, and the prestriate region where Krieter and Singer found a high proportion of cells that exhibited oscillatory firing was predominantly in area MT, which receives strong input from 4B.

The results described here further indicate that when two cells are stimulated by a single contour, or by coherently moving pairs of bars, they show a small increase in correlated firing over what they show when they are stimulated by contours moving in opposite directions. Previous studies in the cat visual cortex also found increased synchrony between cells stimulated by a single contour (Engel et al. 1991c; Gray et al. 1989). The effect described here seems rather small to explain the "binding problem," but the phenomenon may be more robust in unanesthetized animals. Cells 5 mm apart in the cortex showed slightly stronger correlations for pairs with the same orientation selectivity than for cells with different orientation preferences. For cells separated by only 1 or 2 mm, there was no difference in the degree of correlation depending on whether the cells had the same of different orientation selectivities. This is similar to results obtained by Engel et al. (1990), who also saw stronger correlations between cells of similar orientation preferences, but only at longer cortical distances.

The studies by Gray and Singer and by Engel et al. in the cat described interneuronal correlations that took the form of synchronized bursts of firing. Several other cross-correlation

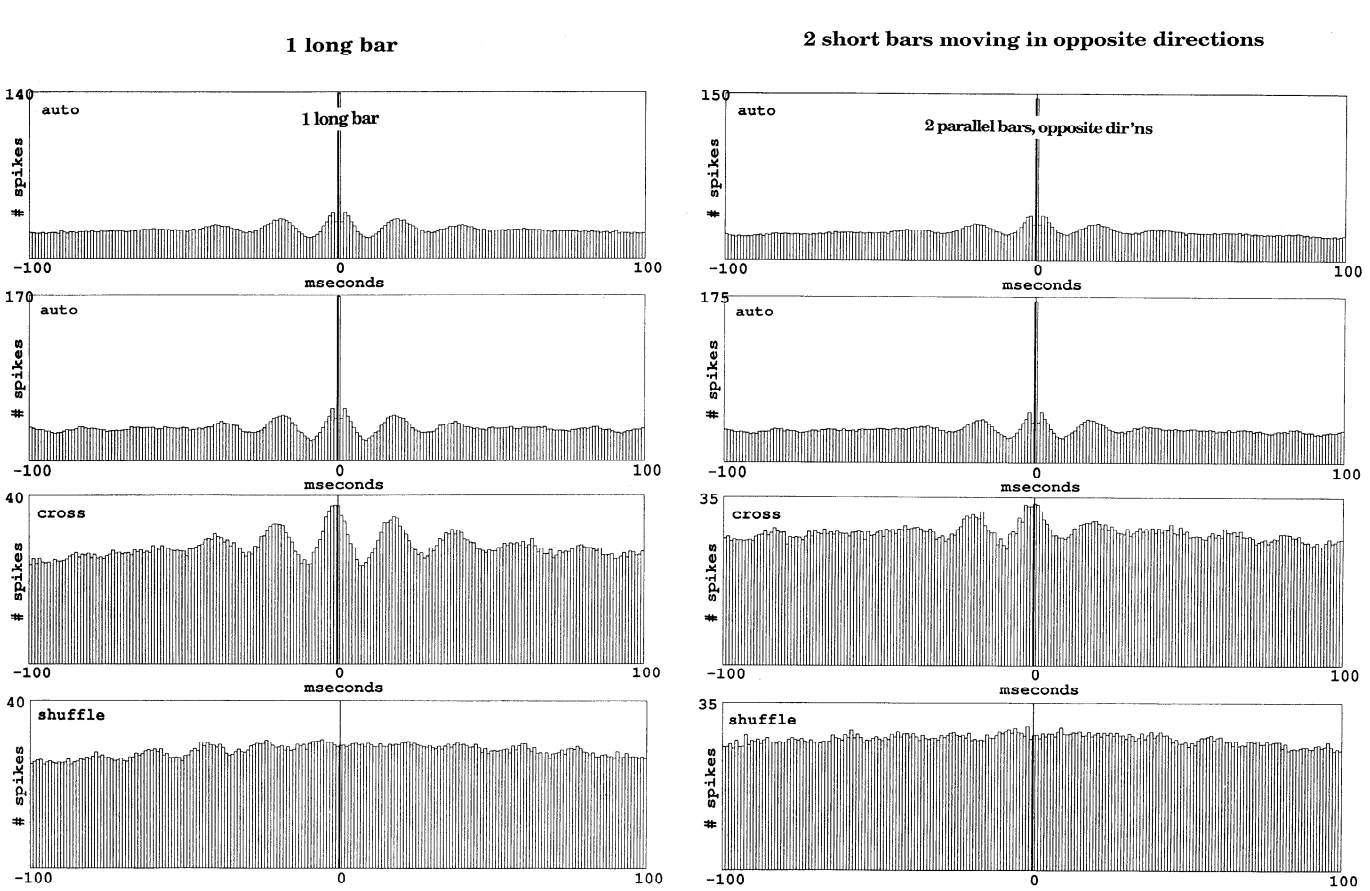

FIG. 15. Averaged correlograms for a pair of deep 3 or 4B cells with the same orientation selectivity, stimulated either with a single long bar, or with 2 short bars moving in opposite directions. Each set of correlograms represents the average of 61 responses. The 2 stimuli were interleaved. Cross-correlation shows slightly stronger synchrony for a single bar than for 2 oppositely moving bars (correlation index for 1 bar = 0.22; correlation index for 2 bars = 0.14). Heights of the 0 ms bins in the autocorrelograms are similar, indicating that the response, the absolute firing rate, was similar for the 2 conditions. For both sets of records the same time interval of 850 ms was used, and $t = \pm 100$ ms.

studies of cat and monkey visual cortex have described neuronal interactions, but either have not noted prominent rhythmicity in the correlations or have explicitly failed to find oscillations (Krüger and Mayer 1990; Toyama et al. 1981; Ts'o et al. 1986; Young et al. 1991). Oscillations are nevertheless very prominent in several other studies: periodic bursty firing in cat striate cortex was reported by Bonds et al. (1989), Eckhorn et al. (1988), Gray and Singer (1989), and Nelson et al. (1989) and was observed in cat area 18 by Hubel and Wiesel in 1965 (Fig. 5). The cross-correlation study of Toyama et al. (1981) does not emphasize periodicities in the correlograms obtained; however, they were interested primarily in synaptic connectivity and excluded cells with periodic firing because they felt that correlated activity in the presence of rhythmic firing need not reflect direct synaptic connectivity but rather the entrained firing of cells linked in a complex network. Toyama et al., nevertheless, did observe periodic firing: they rejected for analysis 23 out of 208 cells "because of the tendency to discharge cyclically." Ts'o et al. (1986) also do not stress oscillatory firing, having apparently rejected cells with periodic autocorrelograms because "they may yield misleading features in the cross-correlogram." Both Toyama et al. and Ts'o et al. averaged over longer times than the German groups (20–30 min as opposed to 100 s) and over such long times that variations in the periodicity may have averaged out the oscillations. Indeed, several of their correlograms do show damped periodic peaks (Ts'o et al. 1986, Figs. 3*a*, 5, and 6). Thus in both these studies, peaks in correlograms that were judged to be nonperiodic might well have exhibited brief periods of regularity that were smeared out over the long averaging periods. Therefore some of the observed correlations might have arisen from complex oscillatory networks, and not solely from direct synaptic connectivity. Finally, Krüger and Mayer (1990) specifically looked for oscillatory firing in their recordings from monkey striate cortex and failed to find any, but, again, their correlograms were calculated for recordings lasting an hour or more.

I have tried averaging responses over various time windows, and find that cells usually show rhythmic firing only for short periods during a response (100–300 ms) even though the response to the stimulus can be longer. The correlograms reveal periodicities only when calculated over short periods. Although the brevity of the oscillatory periods poses significant problems for analysis, it is not inconsistent with perception. Thus I suspect that one rea-

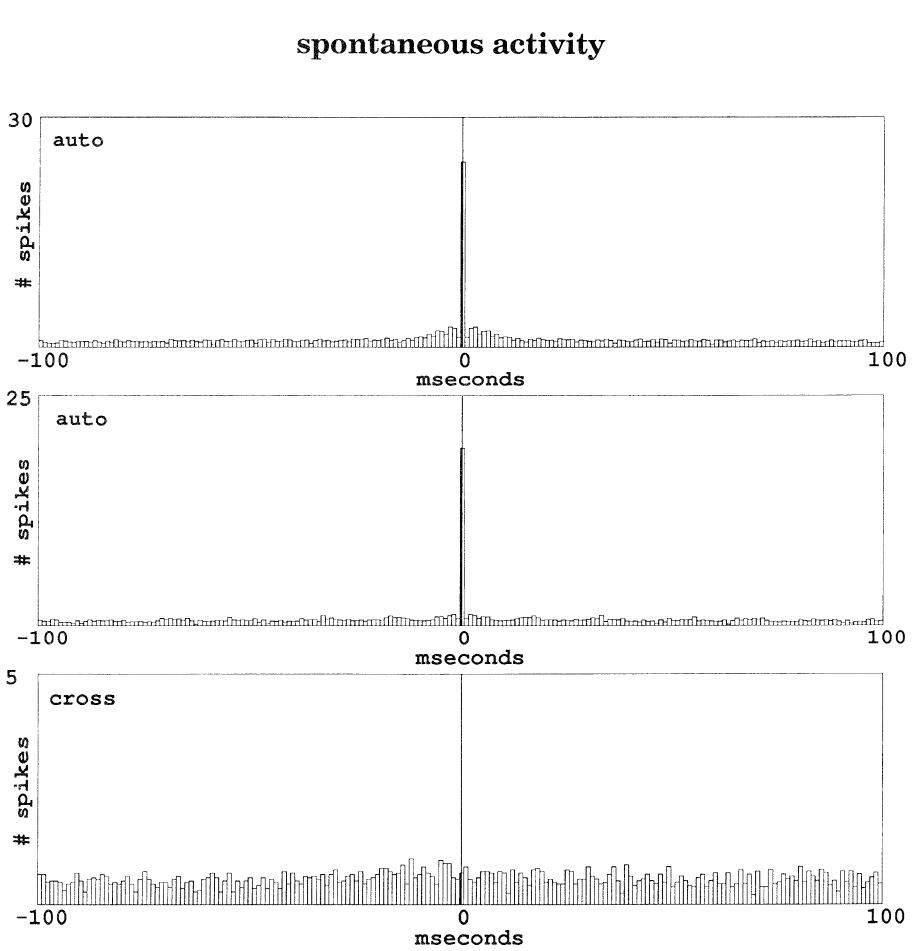

FIG. 16. Averaged correlograms for 30 epochs of spontaneous activity with no visual stimulation, same cells as Fig. 15. As for all the other cells we studied, these showed flat auto- and cross-correlograms in the absence of visual stimulation. T = 900 ms and $t = \pm 100$ ms.

son many studies failed to see oscillatory firing patterns may be that they used long time periods for averaging correlograms.

Several facts suggest that the apparent oscillations do not arise simply from spurious correlations in a random firing pattern. First, the criterion for accepting a correlogram as oscillatory requires that the probability that a given correlogram could have been generated by a random spike train be $<1\%$, and $>1\%$ of the responses showed significant oscillations by this criterion. Second, whenever a single unit showed oscillatory firing, the local field potential recorded from the same electrode almost always showed regular oscillations at the same frequency, indicating that other cells in the vicinity were also firing in the same periodic pattern. Third, in recordings made simultaneously from two nearby cells (by using 2 electrodes with tips ~ 50 μm apart), if both cells fired in bursts, then the bursts were invariably synchronous. Finally, bursts in different layers were correlated, although not synchronous, and cells up to 5 mm apart could show synchronous bursts.

What is the relationship between bursty, or oscillatory firing and interneuronal correlations? I have concluded that oscillatory firing contributes to interneuronal synchronization because I find that the amount of interneuronal correlation covaries with the amount of oscillatory firing in the two cells, and because when two cells both show oscillatory firing, the frequencies of oscillations seem to covary for the two cells, especially when they are stimulated by a single contour. König et al. (1995) recently reported that in cat visual cortex long-range (>2 mm) synchronization between cells is almost invariably associated with oscillatory firing. Engel et al. (1991c) recorded from four electrodes simultaneously and found sites with two cells sharing one orientation tuning and two cells a different orientation preference. When they stimulated with two optimal bars they found that the oscillations of each pair of cells covaried independently. These studies strongly suggest that oscillatory activity and correlated firing are somehow related. It is of course not essential that oscillatory firing be involved for synchronous firing to occur, though feedback activity would seem to offer an ingenious mechanism to enhance, or produce, correlations between neurons. Indeed, a simulation study by König and Schillen (1991) shows that the establishment of zero phase lag synchrony between neurons is easily and rapidly established if cells are entrained into oscillatory firing by recurrent feedback.

To imagine how correlated firing or synchronous oscillations might come about and how they might code relationships between visual inputs, consider an area of cortex in V-1 and the region in Visual area 2 (V-2) to which that part of V-1 projects. When a long vertical contour crosses the visual field, cells of that orientation preference in many hypercolumns will be activated, and in turn activate cells in V-2. A given cell in V-2 can be expected to receive converging input from several V-1 hypercolumns. Activated cells in V-2 can then be imagined to feed back excitation to many

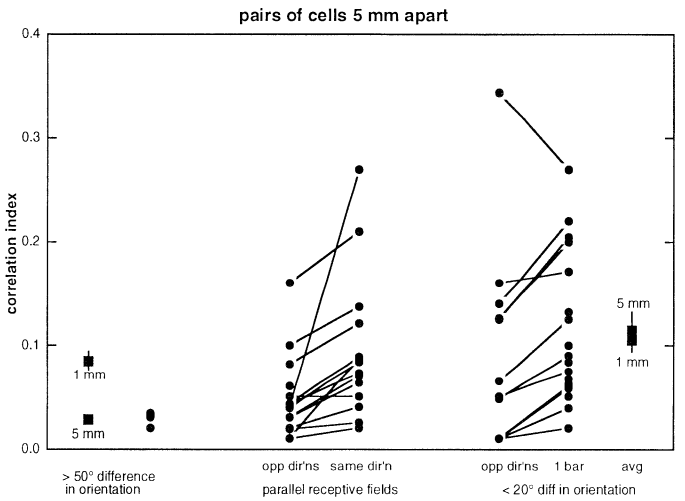

FIG. 17. Summary of 68 cell pairs recorded 5 mm apart in the cortex. Each correlation index was calculated from averaged cross- and shuffled correlograms from at least 20 responses. On average, cells with similar orientation selectivity stimulated with 1 bar showed more synchrony than cells with different preferences, but this difference was at least partly the result of a difference between using 1 or 2 bar stimuli (cells with different orientation preferences were stimulated with 2 bars), because pairs of cells with similar orientation preferences showed stronger synchrony when stimulated with 1 long bar (or 2 parallel bars moving in the same direction) than with 2 bars moving in opposite directions ($P < 0.05$). There was a difference between the correlation index of cells with different orientation selectivities and cells with similar orientation preferences stimulated by 2 bars moving in opposite directions, with the cells with similar orientation selectivity showing stronger correlations, but the difference was marginally significant ($P = 0.056$, 1-tailed t-test). For cells with similar orientation selectivity, the correlation index was larger ($P < 0.05$, paired t-test) if the cells were stimulated either with 2 bars moving in parallel or by a single long bar than if the cells were stimulated with 2 bars moving in opposite directions. The square symbols at the far right and left show the average correlation index (mean ± SE) for all cells with similar (stimulated with 1 bar) or different orientation preferences separated by 2–5 mm or 1–2 mm, as indicated.

vertically oriented V-1 cells (Gilbert and Wiesel 1987; LeVay 1988). Thus a subset of cells in V-1 will become engaged in mutual excitation with cells in V-2. Such a feedback loop could encourage synchrony and oscillatory firing. Synchronous firing will greatly enhance the signal carried by a set of synchronized neurons and could serve as a temporal code for linking responses to spatially separate stimuli.

If synchronized, perhaps oscillatory, firing is used by the visual system for linking features, it would be surprising if other systems, sensory, motor, or higher, did not use similar strategies for linking percepts and ultimately concepts. Indeed, odorant evoked oscillatory activity was first described in the olfactory bulb (Adrian 1942; Freeman 1975), and Lado et al. (1991) and Murthy and Fetz (1991) observed oscillations synchronized between motor and somatosensory cortex in alert monkeys performing a fine motor task. The rhythmic firing in the visual cortex may, alternatively, be an artifact of anesthesia, or simply a means to enhance synaptic efficacy through temporal summation, but the possibility remains that it represents a general cortical mechanism involved in information integration.

The origin of oscillations in the cat is currently a subject of dispute. Oscillations in the firing of cat retinal ganglion cells were observed many years ago (Granit 1933; Kuffler 1953), but only under circumstances in which the condition of the animal was probably very poor. Ghose and Freeman (1990) and Neuenschwander and Singer (1994) have reported oscillatory firing in cat LGN. It is possible that feedback from the cortex could entrain LGN responses to synchrony, which could then be passed on to the cortex. Indeed Sillito et al. (1994) recently described synchronization between pairs of lateral geniculate neurons in the cat, that depended on cortical feedback. Their correlation peaks are much wider (~100 ms) than what has been described in the cat cortex, so geniculate correlations alone probably can't explain the cortical synchronization. Perhaps a similar mechanism of feedback reactivation could explain both cortical and LGN correlations and oscillations. Engel et al. (1991b) have recently reported interhemispheric synchronization in cat V-1 that is eliminated by cutting the corpus callosum, indicating that some cortical correlations are generated by intracortical connections and not by common inputs. The work of Eckhorn et al. (1988) suggests that cortical feedback connections are involved in generating oscillations, but it is also possible that some rhythmicity is generated by local interconnections. The richness and complexity of the networks potentially generating the oscillations may offer an explanation for the variability of the oscillation frequency, because reverberation time might depend on the number of areas involved in the network, which could change instant by instant.

Finding that pairs of cells in different layers can show correlograms peaking at nonzero times might lead one to conclude some particular synaptic relationship between those cells, and indeed the flow of information in the cortex is consistent with the temporal relationships we see here (from layer 4C to deep layer 2/3). Nevertheless, the fact

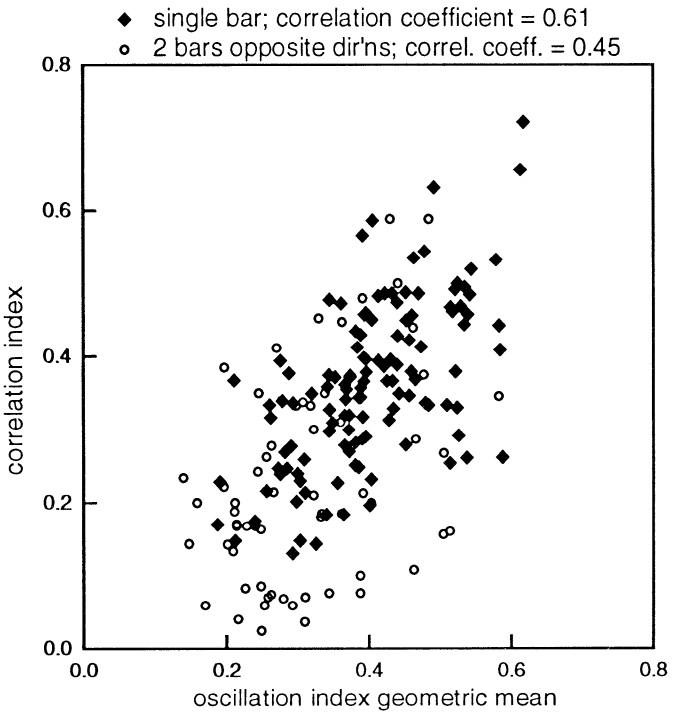

FIG. 18. Correlation between the degree of burstiness in each of 2 cells (layer 4B, 5 mm apart, same orientation) vs. the degree of synchrony between the 2. Abscissa = geometric mean for the 2 cells of the oscillation index (central peak amplitude in each auto-correlogram ÷ the height of the trial-shuffled correlogram).

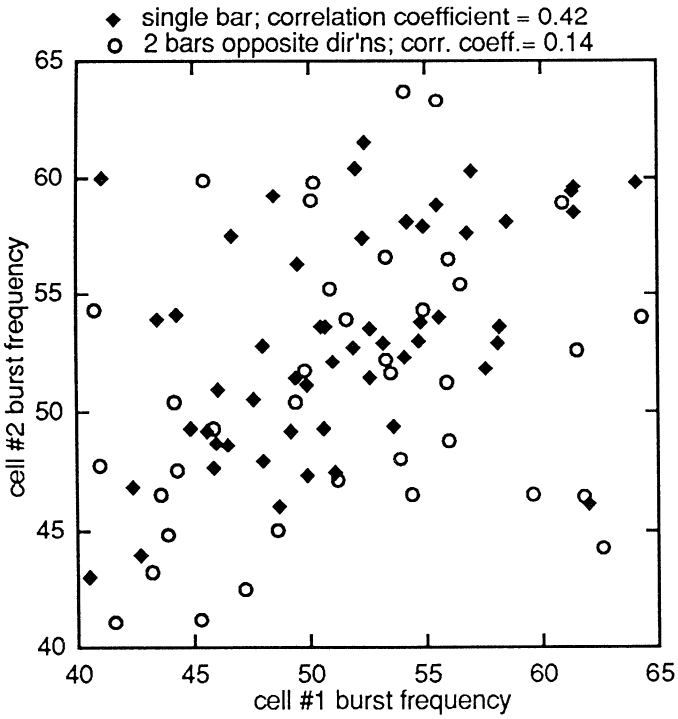

FIG. 19. Correlation between the oscillation frequency (in Hz) in one cell and the oscillation frequency in the other cell, for those 300-ms epochs in which both cells showed strong rhythmicity. Same cell pair as Fig. 18.

that the cells also show rhythmic firing suggests that some more complicated relationship exists.

Many theoreticians seem excited by the idea of stimulus-evoked resonances because for computational models such resonances are a powerful way to produce temporal coherence, and many computational models of the visual system use some kind of resonance or oscillatory activity to link related inputs (Damasio 1989; Grossberg 1980; Grossberg and Mingolla 1985; Johannesema et al. 1986; Koch et al. 1989; König and Schillen 1991; Reitboeck et al. 1989; Sompolinski et al. 1990; Sporns et al. 1989; Wilson and Bower 1990; von der Malsburg and Schneider 1986). If anything, there seem to be more models that use resonances than there are studies on the phenomenon in real animals.

APPENDIX

Both of these calculations were done by P. Dang, M.S. of the Department of Biostatistics at the Harvard School of Public Health.

1. Calculation of the probability that, given 50 numbers with a normal distribution, the largest of these numbers is 4 SD larger than the mean

Assuming that $X_1, X_2, \ldots, X_{50} \sim^{iid} N(m, s^2)$

$P[\max(X_1, X_2, \ldots, X_{50}) > m + 4s]$

$= 1 - P[\max(X_1, X_2, \ldots, X_{50}) < m + 4s]$

$= 1 - P(X_1 < m + 4s \text{ and } X_2 < m + 4s \cdots \text{ and } X_{50} < m + 4s)$

$= 1 - P(X_1 < m + 4s)^{50}$ because of independence of X_is

$= 1 - (0.99996833)^{50}$

$= 0.0015823$

2. In a simulation study, 50 N(0,1) random numbers were generated 10,000 times. The estimated probability was the proportion of times that the maximum of 50 numbers was >4 SD above the mean (both the mean and standard deviation were obtained from the remaining 49 numbers). The resulting probability, $P(\max_{50} > X_{50} + 4s_{50})$, is 0.0058. Thus the probability calculated in the simulation study is about four times larger than the one computed above, but is still <1%.

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