On Oscillating Neuronal Responses in the Visual Cortex of the Monkey

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SUMMARY AND CONCLUSIONS

1. Recent studies of visual processing in the cat have shown stimulus-related oscillations in the 30- to 70-Hz range. We sought to replicate these findings in the monkey.

2. We recorded multunit activity (MUA) and local field potentials (LFP) in areas V1 and middle-temporal area (MT), and MUA from the inferotemporal cortex (IT) of monkeys (Macaca fuscata). Recordings in all areas were made under conditions of anesthesia as close as possible to those in previous studies of oscillating responses in the cat. In addition, we recorded MUA in the IT of behaving monkeys while the monkeys performed a face discrimination task.

3. In areas V1 and MT, LFP power spectra showed broadband increases (1-100 Hz) in amplitude on stimulation by swept optimally oriented light bars, and not a shift in power from low to midfrequency, as has been reported in the cat.

4. MUA autocorrelograms (ACGs), classified by fitting Gabor functions, showed oscillations at ~10% of recording sites in V1 and MT, but these oscillations were in the alpha range (12-13 Hz).

5. MUA ACGs from IT in the anesthetized monkey showed no oscillations.

6. For MUA ACGs from IT in the behaving monkey, only two recording sites (out of 50) showed an oscillating response, with frequencies of 44 and 48 Hz. One oscillating response was associated with stimulus, and the other was associated with the absence of stimulation.

7. The very low incidence in the monkey of oscillating responses in the 30- to 70-Hz range (2 in 424 recordings made at 142 recording sites) and the absence of stimulus dependence suggest that such oscillations are unlikely to serve a function in the monkey, and that there may be a species difference between monkey and cat in the dynamics of neural activity in the visual cortex.

8. We found that methods of classifying responses as oscillating used in some of the studies of the cat may have led to overestimation of both the number of sites showing oscillation and the number of pairs of sites showing phase coherence. These problems arise from the failure to take account of badness of fit between Gabor functions and their corresponding ACGs, and from Gabor functions "ringing" in response to short phasic phenomena that could be consistent with nonoscillatory activity.

INTRODUCTION

Oscillations in neural responses from the visual cortex of the cat have been described recently (Eckhorn et al. 1988; Ghose and Freeman 1990; Gray and Singer 1989; Gray et al. 1989). These oscillations are "stimulus related" because the frequency spectrum during the passage of a stimulus through the receptive field (RF) shows spectral peaks in a frequency range between 30 and 70 Hz, in marked contrast to the low-frequency peaks (1-30 Hz) of background activity (Eckhorn et al. 1988; Gray and Singer 1989). These oscillations are most manifest in local field potentials (LFPs), are less clear in multiple unit spike activity, and are often not pronounced in the spike responses of single units (Eckhorn et al. 1989). Oscillations occur at a variable delay after the onset of stimulation, and their phase at onset is not time locked to the onset of the stimulus (Eckhorn et al. 1988, 1989; Engel et al. 1990; Gray and Singer 1989). Frequency spectra from individual trials show oscillating components at many frequencies (Eckhorn et al. 1988). Often, however, the spectra also show most energy to be distributed in a narrow peak at a single spectral frequency (Eckhorn et al. 1988, 1989; Gray and Singer 1989). The precise frequency of this large peak varies considerably between trials, even when the trials involve the same stimulation (Eckhorn et al. 1989; Engel et al. 1990; Gray and Singer 1989).

Oscillating neural responses recorded at different sites that were up to 8 mm apart can show phase coherence (synchronization) (Eckhorn et al. 1988; Gray et al. 1989; Gray and Singer 1989). The lack of overlap of the RFs of cells in the 2-8 mm electrode-separation range has been exploited to show that the degree of synchronization between distant cortical sites is sometimes related to "global" properties of the stimulus (Gray et al. 1989). Coherence between two recording sites with similar orientation preference is reported to be best when their RFs are stimulated by a single long bar. It is less strong when the two RFs are stimulated by two short bars that are moved in the same direction and is absent when the two short bars are moved in opposite directions (Gray et al. 1989).

This dependence of phase coherence on global stimulus properties has aroused considerable theoretical interest because it might make available phase information as a temporal "code" by which the activity of cells signaling spatially separated features of an object may be transiently bound together (Eckhorn et al. 1988, 1989; Gray et al. 1989; Gray and Singer 1989; Stryker 1989; von der Malsburg and Schneider 1986; Young et al. 1989). These theoretical speculations involve the idea that neurons that signal features of the same object might oscillate in phase, whereas neurons that signal features of different objects might oscillate out of phase.

It has sometimes been assumed that the phase relations of neural responses with respect to a large spectral component are a universal neural code (e.g., Crick and Koch 1990; Damasio 1989; Eckhorn et al. 1988; Sporns et al. 1989). Very few studies, however, have reported compara-
ble frequency spectra from the visual cortex of animals other than the cat. Freeman and van Dijk (1987), in one example, recorded field potentials from an array of subdural electrodes that had been chronically implanted in an adult rhesus monkey. The recordings were made while the monkey performed a fixation task during which a square checkerboard pattern was presented centrally. The power spectra of these data showed that energy was widely distributed over the spectrum from 0.3 to >100 Hz, with most of the energy concentrated in the low-frequency components. In contrast to the frequency spectra of field potentials recorded in the cat, which show narrow high-amplitude components in the 30- to 70-Hz range. There were no significant differences, either in electroencephalogram (EEG) amplitudes or in the frequency domain, between different time regions related to different epochs of the task, in contrast to the stimulus-dependent character of oscillations in the cat.

These differences between the frequency distributions of activity in the cat and those in the monkey could be due to a number of factors. It is possible that the differences could be due to the presence of anesthesia in the cat studies [although very similar oscillating responses have been observed in waking cats and in cats under different types and depths of anesthesia (Gray and Singer 1989)], or to species differences in the characteristics or prevalence of oscillating responses, or to differences of task, the paradigm used for recording or the types of stimulation. The present study was intended to clarify the conditions under which similarities or differences of activity are observed in cat and monkey. This was both to assess the generality of the oscillating phenomena across species, and to determine the suitability of the monkey as an experimental subject for future studies aimed at elucidating the mechanism and functional significance of stimulus-evoked oscillations. We decided, therefore, to employ, in the monkey, an experimental paradigm, analytic techniques, and conditions of anesthesia as similar as possible to those employed in previous studies of stimulus-related oscillations in the cat. We examined responses in a number of areas: V1, because this area is, like cat area 17, the primary visual cortex; the middle-temporal area (MT), because the typical receptive-field size in MT, and this area’s position in the parallel visual hierarchy, are more similar to these properties of cat area 17; the infero-temporal (IT) cortex of the anesthetized monkey because “binding” may be involved in the generation of the complex stimulus specificities that some IT cells possess; and the IT of awake monkeys while they performed a discrimination task to assess the occurrence of oscillations in cells responsive to attended complex stimuli in the absence of any anesthetic.

METHODS

Anesthetized monkey experiments

Four adult Japanese monkeys (Macaca fuscata) were used for recordings under anesthesia. The methods of preparation were the same as those described previously (e.g., Tanaka and Saito 1989; Tanaka et al. 1991). In brief, the monkeys were first prepared for repeated recordings by a single aseptic surgery, which was performed under pentobarbital sodium anesthesia. A brass head-fixation block was secured to the skull. The posterior aspects of the skull in two monkeys, and the right lateral surface of the skull in the two other monkeys, were exposed and covered with dental acrylic to permit later access. Recording sessions, which were separated by an interval of at least 1 wk for each monkey, began with the induction of anesthesia with ketamine hydrochloride (10 mg/kg im), and an injection of atropine sulphate (0.5 mg sc) to reduce salivation. The animal was intubated with an endotracheal cannula coated with xylocaine and antibiotic cream and placed on the experimental stage. The head was secured to an arm of the stage, and a small hole for the microelectrode recording was drilled through the resin-coated skull. After artificial respiration began, the muscle relaxant gallamine triethiodide (initially 10 mg/kg, then 4 mg/kg every hour) was given by intramuscular injection. Anesthesia was maintained by ventilation with a gas mixture of N2O and O2 (60:40 to 80:20) during recordings. The electrocardiogram (ECG) was continuously monitored.

Recording and visual stimulation. Multimultiunit spike activity (MUA) was recorded with the use of a glass-coated “elgiloy” microelectrode (Suzuki and Azuma 1976) having an impedance in the brain of 0.8 MΩ at 1 kHz. In addition, in V1 and MT, LFPs were recorded with the same electrode. Recordings began not less than 5 h after initial anesthesia, to ensure that no effect of ketamine remained. LFPs in the region of the microelectrode were filtered by the signal with a bandpass of 1–100 Hz, and the data were derived by first filtering the raw signal with a bandpass of 0.5–5 kHz. The signal was then sent to a threshold discriminator that passed spike signals only if they exceeded any background noise by a factor of ~2. LFP and MUA data were digitized separately, both at the rate of 1 kHz, and were stored on computer.

The procedure at each recording site in V1 and MT typically involved the determination of the RF of the MUA with various bars and spots, and an assay for ocular-dominance group, disparity tuning, end stopping, degree of orientation preference, preferred orientation, sensitivity to movement direction, color selectivity, and preference for darker-than- or lighter-than-background stimulation. Once these characteristics were established, a stimulus of optimal orientation, size, disparity, color, and contrast polarity was projected onto a translucent screen 1 m in front of the monkey’s eyes. Stimulation was binocular, and the two RFs were brought into spatial register with a prism. The stimulus was then swept back and forth, under computer control, in a direction perpendicular to the preferred orientation across the RF (cf Gray et al. 1989). The stimulus was swept across the RF at four speeds; in the case of recordings in V1, at 1.25, 2.5, 5, and 10°/s; and in the case of MT, at 5, 10, 20, and 40°/s. Each trial lasted 4,000 ms, in which the stimulus moved in one direction in the first half of the trial, and in the opposite direction in the second half. A complete recording at a cortical site was composed of 40 trials, comprising 10 repetitions of each sweep speed.

The procedure at each recording site in IT was to begin by determining the RF and stimulus selectivity of the spike activity. This was done by presenting a large number of solid objects and two-dimensional patterns of varying complexity, and converging on the set of stimuli that excited the cell. With the use of an image processing computer, the effective stimuli were digitized and their components separated to investigate what subset of features of the stimuli were effective (Tanaka et al. 1991). Responses to effective stimuli, which were presented monocularly 10 times for 2,000–3,000 ms with an interstimulus interval of 5–10 s, were analyzed to investigate the possible presence of oscillating responses.

Behaving monkey experiment

A Japanese monkey (M. fuscata) was prepared for repeated recording by implanting, under pentobarbital sodium anesthesia, a stainless steel pipe for head fixation and a stainless steel recording chamber. The monkey was trained to discriminate a small set
of human faces (the "Son" set) from a larger set of faces (the "Soff" set). Each trial of the task involved a 100-ms warning tone followed after a delay of 500 ms by a 600-ms presentation of a face. A green spot was presented 1,000 ms after the offset of the face stimulus for 1,700 ms to serve as a response cue. After a face belonging to the Soff set, the monkey was rewarded with fruit juice if it pushed a key immediately after the appearance of the green spot. After a face belonging to the Soff set, the monkey was rewarded for pressing the key after the offset of the response cue. Further details of the preparation and task have been presented elsewhere (e.g., Yamane et al. 1988, 1990).

Recordings were made with a glass-coated tungsten microelectrode. The locations of the recording tracks were confirmed by later histological examination (Yamane et al. 1988). Presentation was binocular. The number of MUA spike responses to the face stimulus, in a window extending from 100 ms after face onset for 1,000 ms, and that in a 1,000-ms prestimulus baseline window was calculated. If the number of spike responses in the "stimulus-on" window was 400% greater than that in the baseline window, the trial was selected on the grounds that such a response would be expected of cells mediating response to the stimulus, and a "recording" was composed of 10 such responses.

**Statistical methods**

Peristimulus time histograms (PSTH) and the autocorrelation of the MUA at each site were computed, and, where the LFP was recorded, the power spectrum of the fast Fourier transform (ITTT) of the LFP.

LFP power spectra for the recordings in V1 and MT were derived from 512-ms epochs selected from each trial in the following way. Each trial was divided into time windows in which one set of windows (stimulus-on windows) began just before the peaks of the MUA response to stimulus passage in the forward and reverse directions. Further windows, which corresponded to periods in which the stimulus was not in the RF, were also defined. Typically, the first "stimulus-off" window began at the start of the trial, the second began when the MUA PSTH returned to the spontaneous baseline level after the first sweep, and the third began after the MUA returned to baseline after the second sweep. Power spectra were derived by ITTT for each window of each trial. After derivation of the spectra for all trials at a particular site, the spectra were averaged. Averaging was performed in the frequency domain, to take explicit account of possible phase and onset variability of the oscillations between trials in the time domain. The output of this procedure consisted of two frequency spectra corresponding to stimulus-on and stimulus-off conditions for each sweep speed for each recording site.

The LFP power spectra were analyzed by repeated-measures analysis of variance (ANOVA), with factors of frequency band, stimulus (on or off), and stimulus drift speed. The degrees of freedom were adjusted where appropriate by the Greenhouse-Geisser correction, to eliminate the possibility of inflations of type I error which can be associated with repeated measures ANOVA (Keselman and Ragan 1980).

MUA autocorrelograms (ACGs) with 1-ms binwidth were derived in a fashion analogous to the derivation of LFP spectra. Where simultaneous LFP and MUA recordings were made, windows with identical start points and durations were used. ACGs derived from recordings of MUA made in IT (in both the behaving and anesthetized preparation), where the spiking rate was typically lower than in V1 or MT, used windows of 1,000-ms duration to include sufficient spike events. Shift predictors were derived for both stimulus-on and stimulus-off windows by cross-correlating MUA recordings shuffled by one stimulus period to estimate stimulus-locked components in the ACGs (Engel et al. 1990; Perkel et al. 1967a,b), and these were subtracted from the "raw" ACGs.

Averaging across trials was undertaken in the autocorrelation domain and not the time domain, again to take account of possible phase and onset variability of oscillations in the time domain.

To analyze the spike activity data, damped sine waves (Gabor functions) were fitted by nonlinear regression to the ACGs (cf. Engel et al. 1990; Gray et al. 1989). A Gabor function is a cosine wave whose envelope is damped by a Gaussian function, or

$$f(x) = a \cdot \sin \left( b \cdot x + \phi \right) + c$$

The fitting procedure derived estimates of the amplitude offset $a$, the modulation amplitude $b$ of the sine wave; the decay constant (the time after which the envelope of the Gabor function declined to $e^{-1}$ of its maximum), which was derived from $g$; the frequency, from $\lambda$ and phase $\phi$ of the function in $x$ (lag), estimates of the asymptotic standard error for each of these parameters; as well as a value for the proportion of variance in the ACG explained by the Gabor function. Following criteria very similar to those employed in a recent cat study (Engel et al. 1990), ACGs were classified as oscillating if 1) the estimate of the amplitude of the Gabor function was more than twice the estimate of its standard error (i.e., the Gabor function was statistically different from a Gabor function with 0 amplitude at the 5% level)

$$a/\text{set}(a) > 2$$

2) the estimate of the amplitude of the Gabor function was >10% of the estimate of the amplitude offset

$$a/b > 0.1$$

and 3) the quotient of the decay constant over the cycle time was >0.8 (i.e., there were at least 3 peaks in the Gabor function)

$$[(2/g^2)/i(2\pi)/2] > 0.8$$

In addition, however, in cases where the amplitude of the Gabor function was more than twice its standard error but the Gabor function fitted the ACG only very poorly (i.e., when the Gabor function explained little of the variance in the ACG), the parameters of the Gabor function were considered to be unreliable estimates of the variability in the ACG, and the ACG was, therefore, not classified as oscillating (see DISCUSSION). We arbitrarily chose a threshold for acceptance that the Gabor function fitted the ACG tolerably well at 20% variance explained (allowing 80% of the variance in the ACG to remain unaccounted for by the Gabor function). Criterion 4 was therefore that the variance-explained statistic exceeded 0.2.

If the parameters of a description are to be used to classify something, the description should fit the described thing well. Notwithstanding this, to be certain that criterion 4 did not give rise to type II error (classification as "not oscillating" when oscillation was present), due to, for example, the presence of high frequency noise, we examined those responses that were rejected only by criterion 4 after a pass of a 1:1:1 smoothing routine (cf. Gray et al. 1990). Responses that satisfied all criteria after smoothing were accepted as oscillating.

**RESULTS**

**Area VI**

A subset of the data recorded under anesthesia in area VI, at which recordings with all four drift speeds were undertaken, was selected. This subset comprised 104 recordings at 26 sites, at 18 of which LFP data was also recorded (2 monkeys).

LFPs. All frequency spectra of the LFPs showed the greater part of their power to be concentrated in the low-frequency
components, as illustrated by the representative spectra from one site in Fig. 1. The form of the spectra was, in all cases, very similar to the shape of a reciprocal function with increasing frequency ("1/f noise"), in which respect the LFP power spectra were very similar to the EEG spectra reported for behaving monkey (e.g., Freeman and van Dijk 1987). Deviations from the 1/f noise form were apparent only in the alpha range, where there was generally more power than would have been expected in both stimulus-on and stimulus-off spectra, and in the region of 50 Hz. The small component around 50 Hz was not statistically related to stimulation or to any other variable and remained at exactly the same frequency in all spectra. We assume that it was due to a constant background electrical interference. The small size of this blip suggested that this noise was almost completely eliminated, but that it was still just detectable in the LFP frequency distributions.

The typical differences between stimulus-on and stimulus-off spectra appeared to consist of a broadband increase in power in the stimulus-on spectra (compare Fig. 1, A with B). The ANOVA analyses performed on spectra from all sites at which LFPs were recorded showed that there were significant differences between the amplitudes of frequency components in the stimulus-on and stimulus-off windows in frequency bands between 1 and 6 Hz, and to a lesser extent in every band from 25 to 100 Hz. In every case the stimulus effect was characterized by greater power in the spectra associated with the stimulus-on condition. It was not, therefore, the case that stimulation was associated with a shift of spectral power from low to higher frequency bands, as is the case in the cat (Eckhorn et al. 1988; Gray and Singer 1989). Indeed, the effects were almost the opposite: stimulation was associated with increases in power particularly at the low frequencies with a smaller increase across almost the entire spectrum from 1 to 100 Hz. Figure 2 illustrates this by showing the average difference spectrum for all the recordings made in V1.

Over the 10- to 20-Hz range, a nonsignificant diminution of power occurred during stimulation. This frequency region is centered on the alpha range, and it is possible that the slight reduction in spectral power in this band was due to the diminution of alpha activity by the stimulus.

This very wide frequency distribution of stimulus-related frequency components differs from the frequency distributions observed in the cat in a further respect. Frequency spectra recorded from cat visual cortex show sharply peaked components in the 30- to 70-Hz band (e.g., Eckhorn et al. 1988), whereas these spectra clearly do not. We thought it possible that variability in the peak frequency of stimulus-evoked oscillations between trials might have contributed to this wide frequency distribution of the stimulus effects in the present data.

Accordingly, single-trial frequency spectra derived from stimulus-on periods were analyzed for evidence that sharp peaks were present. Examination of the frequency spectra reported from studies of the cat (e.g., Eckhorn et al. 1988; Gray and Singer 1989) showed that amplitudes of frequency components near a peak typically exceed four times the amplitude of components only 10 Hz away. We adopted the more liberal criterion that a peak was present if any frequency component exceeded twice the amplitude of components 10 Hz away. The single-trial spectra were digitally filtered with a bandpass between 20 and 100 Hz to
**Table 1. Sites and recordings in area V1 fitted by Gabor functions classified as oscillating**

<table>
<thead>
<tr>
<th>Site</th>
<th>Stimulus Off Hertz</th>
<th>$r^2$</th>
<th>Stimulus On Drift, deg/s</th>
<th>Hertz</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>os0412.15</td>
<td>13</td>
<td>0.11 (0.24*)</td>
<td>Not oscillating</td>
<td></td>
<td></td>
</tr>
<tr>
<td>os0412.17</td>
<td>Not oscillating</td>
<td>5</td>
<td>13</td>
<td>0.38†</td>
<td></td>
</tr>
<tr>
<td>os0412.21</td>
<td>Not oscillating</td>
<td>10</td>
<td>81</td>
<td>0.06 (not oscillating)</td>
<td></td>
</tr>
<tr>
<td>os0530.10</td>
<td>Not oscillating</td>
<td>10</td>
<td>12</td>
<td>0.11 (not oscillating)</td>
<td></td>
</tr>
<tr>
<td>os0530.17</td>
<td>not oscillating</td>
<td>2.5</td>
<td>13</td>
<td>0.53†</td>
<td></td>
</tr>
</tbody>
</table>

Frequency and variance-explained parameters corresponding to stimulus off (at left) and stimulus on (at right) autocorrelograms (ACGs) for any response in area V1 that satisfied criteria of Engel et al. (1990) as being oscillatory. Only those recordings, however, that were characterized by Gabor functions, which fitted their ACGs tolerably well (~20% variance explained), are classified as oscillating in this study. Notes in parentheses beside responses rejected by criterion 4 indicate results of smoothing with a 1:1:1 routine. "Not oscillating" in this context, means that after smoothing the ACG did not give rise to Gabor function that passed criteria of Engel et al. (1990), whereas values correspond to "after smoothing" variance-explained statistics of those responses that did pass the Engel et al. (1990) criteria after smoothing. *Response satisfied 4 criteria for classification as oscillating response only after smoothing.

exclude the large-amplitude low-frequency components (cf. Gray and Singer 1989). By this criterion, 25% of the single trials showed a spectral peak. The distribution of the frequencies at which these peaks were present, however, showed that most peaks were at the lowest frequency end of the submitted bandwidth. Indeed, a regression analysis showed that a reciprocal function of frequency explained 89.5% of the variance in the distribution of single-trial peak frequencies ($P < 0.001$). This concentration of the frequencies of single-trial peaks in the low-frequency part of the spectrum shows that intertrial variability in the peak frequency of oscillating components could not have given rise to the wide frequency distribution of the stimulus effects.

MUA. Only a small fraction of the ACGs exhibited oscillating responses according to the applied criteria, as set out in Table 1. Five out of the 104 recordings at 26 sites showed ACGs that would have been classified as oscillating according to the criteria of Engel et al. (1990), but only three ACGs, which were also fitted tolerably well by their Gabor functions, are classified as oscillating here. Of these three responses, one fitted satisfactorily only after smoothing.

None of the small proportion of the reliable oscillating responses was in the 30- to 70-Hz frequency band. The reliably oscillating responses were in the alpha range (see Fig. 3A). A large proportion (40%) of the Gabor functions that would have been accepted as oscillating according to the criteria applied in Engel et al. (1990) can be seen to be poor descriptors of the variability in the ACGs. After smoothing, these ACGs were not classified as oscillating even by the criteria of Engel et al. (1990). This was because smoothing diminished a large initial transient in the ACG that had given rise to an apparently oscillating Gabor function when fitted unsmoothed.

**Area MT**

A subset of the data recorded under anesthesia in area MT was selected, which comprised all recordings for which all four drift speeds had been employed. This subset comprised 120 recordings at 30 sites, at all of which LFP data were also recorded (2 monkeys).

**LOCAL FIELD POTENTIALS.** All frequency spectra for recordings in MT showed most power to be concentrated in the

FIG. 3. Oscillating autocorrelograms (ACGs) from (A) V1, (B) middle-temporal area (MT) (anesthetized monkey), and (C) inferotemporal cortex (IT) (awake, behaving monkey) together with their corresponding Gabor functions. A and B: oscillations in the alpha range (12–13 Hz). C: the only oscillation in the gamma range (44 Hz) that was associated with the stimulus-on condition.
low-frequency component and took a form similar to 1/f noise (see Fig. 4). There were significant differences between the spectra for stimulus-on and stimulus-off windows of the PSTH in ANOVA analyses on the basis of frequency bands between 1 and 6 Hz, and in every band between 45 and 100 Hz. In all bands except those in the region of alpha activity, the stimulus effect took the form of greater power associated with the stimulus-on condition. In the alpha range there was a significant diminution of power on stimulation. As in V1, therefore, it was not the case that stimulation was associated with a transfer of power from the low-frequency components of the spectrum to the mid-frequency components. Rather, there was a wideband increase in power on stimulation, at all frequencies except those centered on the alpha range, which was particularly evident at the lowest frequencies (see Fig. 5).

We examined the single-trial LFP power spectra to establish whether the wide distribution in frequency of stimulus effects could be due to narrow, but frequency-variable, peaks being present. Even using the same relaxed criteria as those employed on V1 single-trial power spectra, only 17% of trials showed a spectral peak, and again the distribution of the peak frequencies was skewed toward the lowest sub-

![FIG. 4](https://example.com/image4.png)  
**FIG. 4.** Example LFP spectra drawn from the stimulus-off periods (B) and from the stimulus-on periods (A) of the responses recorded at a site in area MT. Except in the alpha range, where there is more power than would be expected, the form of the spectrum as a function of frequency is similar to a reciprocal function of frequency for both stimulus-on and stimulus-off periods. As in the V1 data, there was no shift in power from the low frequency to midfrequency components.

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 unreliable indicants of the occurrence of oscillation in the responses. After smoothing, two of these responses failed the criteria of Engel et al. (1990), because of the diminution by smoothing of a large initial transient that had evidently given rise to an apparently oscillating Gabor function in the unsmoothed analysis. The other ACG (ts0410.31), however, passed all four criteria as an oscillating response. But this response (see Fig. 7B) was characterized by an initial "burst" component followed by an "inhibition" component, which, after a return to mean firing, was followed by a flat ACG. This response therefore contained no sustained oscillatory component and will be considered in the DISCUSSION.

**Behaving monkey IT cortex: MUA**

Responses from only 2 of the 50 sites studied in the behaving monkey IT oscillated (Table 4). One response showed oscillation in association with the stimulus-on condition, its

**TABLE 3. Sites and recordings in anesthetized monkey IT fitted by Gabor functions classified as oscillating**

<table>
<thead>
<tr>
<th>Site</th>
<th>Hertz</th>
<th>$r^2$</th>
<th>Hertz</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>ts0410.31</td>
<td>74</td>
<td>0.08 (0.36*)</td>
<td>Not oscillating</td>
<td></td>
</tr>
<tr>
<td>ts0410.33</td>
<td>78</td>
<td>0.06 (not oscillating)</td>
<td>Not oscillating</td>
<td></td>
</tr>
<tr>
<td>ts0517 32</td>
<td></td>
<td></td>
<td>81</td>
<td>0.12 (not oscillating)</td>
</tr>
</tbody>
</table>

Frequency and variance-explained parameters corresponding to stimulus-off and stimulus-on ACGs for any response in the IT (inferotemporal) of an anesthetized monkey that satisfied the criteria of Engel et al. (1990) as being oscillatory. After smoothing, 2 of these recordings failed to pass the criteria of Engel et al. (1990). *One ACG, however, that would have been classified as oscillating by all the criteria after smoothing was an example of the possible misclassification of short phasic phenomena as oscillations, and this case is illustrated in Fig. 7B and noted in the DISCUSSION.

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Responses from only 2 of the 50 sites studied in the behaving monkey IT oscillated (Table 4). One response showed oscillation in association with the stimulus-on condition, its

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<table>
<thead>
<tr>
<th>Site</th>
<th>Hertz</th>
<th>$r^2$</th>
<th>Hertz</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>151128.2</td>
<td>Not oscillating</td>
<td>80</td>
<td>0.05 (not oscillating)</td>
<td></td>
</tr>
<tr>
<td>171127.2</td>
<td>Not oscillating</td>
<td>29</td>
<td>0.13 (0.07)</td>
<td></td>
</tr>
<tr>
<td>211206.1</td>
<td>51</td>
<td>0.16 (not oscillating)</td>
<td>Not oscillating</td>
<td></td>
</tr>
<tr>
<td>211207.1</td>
<td>48</td>
<td>0.06 (0.27*)</td>
<td>Not oscillating</td>
<td></td>
</tr>
<tr>
<td>391203.1</td>
<td>Not oscillating</td>
<td>44</td>
<td>0.21†</td>
<td></td>
</tr>
<tr>
<td>442125.2</td>
<td>Not oscillating</td>
<td>90</td>
<td>0.04 (0.11)</td>
<td></td>
</tr>
<tr>
<td>481207.1</td>
<td>Not oscillating</td>
<td>46</td>
<td>0.15 (not oscillating)</td>
<td></td>
</tr>
<tr>
<td>511128.1</td>
<td>Not oscillating</td>
<td>83</td>
<td>0.06 (0.14)</td>
<td></td>
</tr>
</tbody>
</table>

Frequency and variance-explained parameters corresponding to stimulus-off and stimulus-on ACGs for any response that satisfied the criteria of Engel et al. (1990) as being oscillatory. *Only those recordings, however, that had Gabor functions that fitted their ACGs tolerably well are classified as oscillating. Conventions for information in parentheses relating to the results after smoothing are as the legend to Table 1. *Response satisfied the 4 criteria for classification as an oscillating response only after 1 pass of a 1:1:1 smoothing routine.

Gabor function having a frequency of 44 Hz (Fig. 3C), whereas the other oscillated in association with the stimulus-off condition with a frequency of 48 Hz (only after smoothing).

The other six of the eight Gabor functions that would have been classified as indicating an oscillating response, however, were very poor descriptors of variability in their ACGs. Of these rejected responses, three were classified as not oscillating after smoothing because of the diminution of the initial transients that had given rise to apparently oscillating Gabor functions in the unsmoothed analyses. Three other rejected Gabor functions were classified as oscillating by the criteria of Engel et al. (1990) after smoothing but still did not explain 20% of the variability in their ACGs.

The results of analyses of MUA recorded in V1, M1, and IT in the anesthetized monkey and IT in the behaving monkey are summarized in Table 5.

**DISCUSSION**

At our point of entry in this study, there were many possible factors responsible for the apparent differences between oscillating phenomena in the cat and the reported distribution of frequency components in the monkey (e.g., Freeman and van Dyck 1987). Our recordings in area V1, which used conditions of stimulation and anesthesia as close as possible to those employed in studies of the cat, showed no evidence for the same oscillating phenomena reported in those studies. Rather than a shift of spectral power from low (1–30 Hz) frequencies to higher (30–70 Hz) frequencies, during which narrow peaks of spectral power appeared, to which local MUA were synchronized, we saw a wideband increase in spectral power with no narrow frequency components and, concomitantly, no statistically reliable midfrequency oscillations in the MUA. This was not a finding of no effect (which would not distinguish between possible insensitivity of the statistical analysis with the absence of the phenomenon): the stimulus effect in the LFP analyses was statistically reliable in all frequency bands (except those centered on the alpha range in V1), and the statistical procedures were able to detect oscillations at frequencies different from those observed in the cat. This wideband stimulus-related increase in spectral

**TABLE 5. Proportion of sites and recordings showing oscillating neuronal responses in areas V1, MT, and in IT**

<table>
<thead>
<tr>
<th>Sites</th>
<th>Stimulus Off</th>
<th>Stimulus On</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1</td>
<td>1/26 (4)</td>
<td>2/26 (8)</td>
</tr>
<tr>
<td>M1</td>
<td>2/30 (7)</td>
<td>4/30 (13)</td>
</tr>
<tr>
<td>IT (anesthetized)</td>
<td>0/36 (0)</td>
<td>0/36 (0)</td>
</tr>
<tr>
<td>IT (behaving)</td>
<td>1/50 (2)</td>
<td>1/50 (2)</td>
</tr>
<tr>
<td>Recordings</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V1</td>
<td>1/104 (1)</td>
<td>2/104 (2)</td>
</tr>
<tr>
<td>MT</td>
<td>2/120 (2)</td>
<td>4/120 (3)</td>
</tr>
<tr>
<td>IT (anesthetized)</td>
<td>0/150 (0)</td>
<td>0/150 (0)</td>
</tr>
<tr>
<td>IT (behaving)</td>
<td>1/50 (2)</td>
<td>1/50 (2)</td>
</tr>
</tbody>
</table>

Proportions of ACGs that we classified as oscillating, given as a proportion of sites and as a proportion of recordings. Values in parentheses are percentages.
power in the recordings in V1 could simply reflect the fact that cells near the electrode fire more strongly when stimulated than when not, and do so at a variety of frequencies: we do not believe that these increases need reflect any more special process.

Area V1 of the monkey brain, however, is not a precise homologue of cat area 17. For example, the receptive fields of cells in monkey V1 are much smaller than those in the cat, and, although cat area 17 is one of several areas to which the cat's lateral geniculate nucleus (LGN) projects, monkey V1 is almost the sole recipient of geniculocortical fibers (Van Essen 1985). Thus monkey V1 is a station in a serial stream from LGN, whereas cat area 17 is one of several areas innervated in parallel. Differences in either the RF size or the organization of inputs and outputs to a visual area might, we thought, have given rise to the observed differences in the occurrence of oscillation. Accordingly, we made recordings in area MT, where both the typical RF size and the input-output organization might more closely mirror those of cat area 17.

Recordings of LFP and MUA in area MT, however, showed a very similar pattern to those made in V1. There was again a broadband increase in LFP spectral power on stimulation, and not a shift of power from low to higher frequencies. The spike activity data showed statistically reliable oscillations only in the alpha range, and there was scant evidence that these oscillations were stimulus related.

The postulated function of stimulus-related oscillatory activity is in the binding together of spatially separate features, and we therefore wondered whether monkey V1 and MT do not exhibit oscillatory activity because they do not participate in the binding process. The necessity for feature binding might exist, for the monkey, only in the "form processing" stream (Ungerleider and Mishkin 1982) beyond V1, where cells signaling the component features of a pattern presumably have their activities "assembled" to give rise to the response properties of cells with more complex specificities that are found in IT (Desimone et al. 1984; Gross et al. 1972; Tanaka et al. 1991; Yamane et al. 1990) and in the superior temporal sulcus (Bruce et al. 1981; Perrett et al. 1982).

Accordinly, we investigated MUA spike activity in the IT of a monkey maintained under conditions of anesthesia almost identical to those employed in studies of these phenomena in the cat. Here, however, we could detect no statistically reliable oscillations at any frequency. The absence of any oscillating components in the IT of the anesthetized preparation further reduced the number of our explanations for the differences between the dynamics of cat and monkey visual cortex: monkeys and cats might react differently to the same anesthetic agents, or there might be a generic difference in the characteristics of neuronal spike trains between the monkey and the cat, or the "spotlight of attention" (Crick 1984) might be necessary for the evocation of oscillations in the monkey, in contrast to the fact that no such attentional process is evidently necessary in the cat. To distinguish these possibilities, we investigated the responses of IT cells in behaving monkeys performing a task on attended complex stimuli.

Recordings taken in behaving monkey IT, while the monkey performed a discrimination task involving the presented stimuli, revealed almost as few oscillatory responses as in the anesthetized preparation. Only 2 of 50 records showed statistically reliable evidence of oscillating responses. These oscillations, however, were in the same frequency range as that of the stimulus-related oscillations that have been described in cat visual cortex. The fact that the only statistically reliable oscillating responses in the 30- to 70-Hz region occurred in the unanesthetized preparation might suggest a small suppressive effect of anesthesia, or of the absence of attention, on oscillatory activity of this frequency in the monkey. Alternatively, the notable rarity of oscillating responses in this frequency band, even in conditions that would be thought to require the binding of attended features into a representation coherent enough to form the basis on which the discrimination decision could be made, and the fact that such oscillations were not stimulus dependent, may suggest that oscillatory activity is not required for feature binding in this region of the monkey visual system.

Methodological problems in classifying recordings as exhibiting oscillating responses and phase coherence

The variety of methods employed to evaluate statistically the presence of oscillation in auto- and cross-correlograms, even in a single laboratory (e.g., Engel et al. 1990; Gray et al. 1989, 1990), illustrates the difficulty involved.

The earliest method (Gray et al. 1989) applied three criteria. First, the amplitude of the sinusoidal component of the Gabor function must be significantly different from zero; second, the amplitude of this modulation must exceed 10% of the amplitude of the shuffled correlogram (offset); and, third, there must be at least three peaks in the Gabor function. A refinement of this method (Engel et al. 1990) applied identical first and second criteria, but the requirement that the quotient of the decay constant over the cycle time of the Gabor function exceeded 0.8 was substituted for criterion three, presumably to avoid any subjective inconsistencies in deciding when three peaks were present.

From our perspective, both these methods are careful approaches to the classification problem. In neither case, however, was account taken of the goodness of fit between the Gabor function and the correlogram. In the nonlinear regression procedure, estimates of the parameters, including the amplitude and the standard error of the sinusoidal component, are made at the asymptote of the regression (i.e., when the Gabor function fits the correlogram about as well as it can). A standard error of the modulation amplitude of the Gabor function sufficiently low to allow the correlogram to be classified as oscillating may still be associated with very bad fit between the Gabor function and the correlogram, as illustrated in the variance-explained statistics of Tables 1-4. In the case that a Gabor function explains only 4% of the variance in the correlogram (leaving 96% unexplained), the parameters of the Gabor function can hardly be reliable evidence that the null hypothesis (that there are no oscillating components present) can be rejected: a Gabor function associated with a low variance-explained statistic is not a reliable indicator of the presence of oscillation in the correlogram.
This issue is illustrated in Fig. 6, which shows an ACG that was fitted by a Gabor function that would have been classified as oscillating if no account were taken of the goodness of fit between the Gabor function and variability in the ACG. In the illustrated case the Gabor function explains only 6% of the variance in the ACG, leaving 94% of the variance unaccounted, a badness of fit that can be seen clearly.

A second problem with these methods concerns possible misclassification of some phenomena in correlograms as oscillations. A burst component is often seen in correlograms. Similarly, a delayed suppression indicative of inhibition can be present. A natural subsequence of inhibition is a return to mean firing. These burst and "delayed inhibition" and "return" components are illustrated schematically in Fig. 7A, and an example from the IT (anesthetized) data is shown in Fig. 7B. In a sense, a biphasic burst, inhibition, and return pattern is a very short oscillation, but such short phasic phenomena, extending over only \( \sim 20 \) ms, could be consistent with being in the chaotic, or stochastic, domain and not only the oscillatory, or limit cycle, domain.

Unfortunately, when a Gabor function is fitted to a correlogram exhibiting this pattern, but which has no sustained oscillatory component at all (as in Fig. 7), the fitted Gabor function can take a form that would cause the correlogram to be classified as oscillating. The problem arises because of the Gabor function "ringing"; in fitting the early phasic part of the correlogram, the function is not damped sufficiently to exclude fitting subsequent sinusoidal modulations, even where there is demonstrably none in the correlogram. Figure 7A also illustrates the fact that, for a decay constant/cycle time ratio at the threshold of acceptance (0.8) (Engel et al. 1990), a "third peak" in a Gabor function may be classified as indicating oscillation when it is very small indeed.

These problems are also poignant for a third method for assessing the presence of oscillation (Gray et al. 1990). In this method the correlogram was first "low-pass filtered" by two passes of a 1:1:1 smoothing routine, and the latencies and amplitudes of the first peak and trough in the correlogram were then ascertained. An estimate of the offset amplitude was derived by calculating the average of the number of spikes in the 5- to 60-ms time-lag bins. The frequency of any oscillatory response was calculated by simply taking the reciprocal of the latency of the first peak in the correlogram. Similarly, the modulation amplitude was simply the first trough to first peak amplitude. Responses were classified as oscillating if the modulation amplitude exceeded

![Fig. 6](image)

**Fig. 6.** Illustration of the issue of badness of fit between Gabor functions and their ACGs. The ACG has no obvious oscillatory component but was fitted by a Gabor function that would have caused the response to be classified as an oscillation by the criteria of Engel et al. (1990). Despite meeting the Engel et al. (1990) criteria, however, the Gabor function fitted the ACG very badly, explaining only 6% of the variance in the ACG. This case may also illustrate the peaks and troughs that could result from a short sample of a spike train in which there is no phasic temporal structure.
10% of the offset amplitude and if the ACF had at least one secondary peak (Gray et al. 1990).

This method depends on four subjective judgements: first, of the latency of the first peak; second, of the amplitude of the first trough; third, of the amplitude of the first peak; and fourth, of whether at least one secondary peak was present. The method is particularly vulnerable to misclassification of the short phasic components discussed immediately above because most of the parameters of an "oscillating response" are derived from informal inspection of just this region of the correlogram. For example, the first peak in the correlogram could be simply the "return" component after inhibition; a component whose presence is wholly consistent with nonoscillatory dynamics. The derivation of the frequency parameter of an oscillatory response from picking the latency of this peak is therefore qualifiable. The only check on misclassifying these short phasic components as indications of a sustained oscillation spindle is the subjective judgement that a secondary peak is, or is not, present.

A more general problem, not limited to any particular method of analysis, derives from the issue of sampling. Because oscillations occur in "spindles" of short duration, the time windows on which analyses are based must be short to avoid oscillatory activity being "washed out" of the ACG by relatively longer periods of nonoscillatory activity. But even if the probability distribution of spike activity is flat (i.e., there is no temporal structure in the spike train), a short sample of the spike train may exhibit peaks and troughs in the ACG because of sampling error. We wonder whether this problem may relate to the observation by Ghose and Freeman (1990) that oscillations were more common in responses with relatively few spike events.

To summarize these methodological issues, we have discussed possible problems associated with accepting Gabor functions that fit their correlograms very badly as indications of oscillation, with Gabor functions ringing in such a way as to extend short phasic phenomena in time into the appearance of oscillation, misclassification of short phasic phenomena as indicators of oscillatory activity, and the problem of sampling. For these reasons, a concern must be that, in some previous studies of oscillating phenomena in the cat, both the proportion of sites with oscillating responses and the proportion of pairs of sites showing phase coherence have been overestimated to an unknown degree.

This possible overestimation may help explain some inconsistencies in reports from different laboratories concerning the proportion of sites in cat visual cortex showing oscillating responses. For example, Toyama et al. (1981) reported only 10% of sites from a cross-correlation study on the grounds that they showed evidence for oscillation. This proportion is qualitatively similar to the information from a different laboratory that oscillating responses are encountered "only occasionally" (C. D. Gilbert in Barinaga 1990). Ghose and Freeman (1990) reported 35% of sites to be oscillating with the use of a method that applied Fourier analysis to the correlograms. In sharp contrast to these reports, the proportion of sites showing oscillation assessed by the methods discussed above ranges as high as 68% (e.g., Engel et al. 1990; Gray et al. 1989).

Overestimation in the present data, because of the inclusion of ill-fitting Gabor functions alone, would have ranged between 17% overestimation (MT) and 100% overestimation (IT, anesthetized). Although we do not dispute that there are sometimes oscillations in cat visual cortex, an interesting question for the future concerns whether the presently understood characteristics of oscillating neural responses in the cat will be reproduced in studies that take account of these difficulties.

Conclusions

These results suggest a difference between cat and monkey in the dynamics of neural activity in visual cortex. There was a different change in the frequency distributions of LFPs on stimulation in the monkey than that in the cat. Concretely, the changes in frequency distribution that we saw in the monkey would not provide narrow band high-amplitude field potentials to which spike activity could become synchronized. Concomitantly, there was very little evidence from spike recordings that stimulus-related oscillating neuronal responses are present in monkey visual cortex. If this absence of stimulus-related oscillating responses from monkey visual cortex were confirmed, it would seem to us unlikely that stimulus-related oscillations could be a general phenomenon, and unlikely, therefore, that a periodic temporal "code" is a general solution to the problem of binding the spatially separate features of an object into a coherent representation. Whatever the mechanism by which features are bound together, at least in the monkey, we suppose that it is probably not one involving periodic temporal structure in neuronal spike trains, and its nature must be elucidated in future research.

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