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Stimulus-Dependent Neuronal Oscillations in Cat Visual Cortex: Receptive Field Properties and Feature Dependence

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Abstract

Previously we have demonstrated that neurons in the striate cortex of lightly anaesthetized cats exhibit oscillatory responses at a frequency near 50 Hz in response to their preferred stimuli. Here we have used both single and multiple unit recording techniques to determine: (i) the receptive field properties and laminar distribution of cells exhibiting oscillatory responses; and (ii) the influence of changing stimulus properties on the temporal behaviour of the oscillatory responses. Oscillatory responses were detected and evaluated by computation of the autocorrelation function of the neuronal spike trains. We recorded oscillatory responses in 56% of the standard complex cells and in 12% and 11% of the simple and special complex cells. Cells exhibiting oscillatory responses were located primarily in supra- and infragranular layers. The oscillatory modulation amplitude of the autocorrelation function was enhanced by binocular stimulation (9 out of 16 cells) and reduced by combined stimulation with optimal and orthogonally orientated light bars (16 out of 21 cells). Changing stimulus orientation caused no change in the oscillation frequency of the sampled population of cells, while oscillation frequency increased monotonically with respect to stimulus velocity within the range of 1 – 12 degrees per second (10 out of 11 cells). The oscillatory modulation of the autocorrelation function increased as a function of stimulus length within the boundary of the cell's receptive field (11 out of 11 cells). In 6 out of these 11 cells, the responses did not show an oscillatory modulation if elicited by small moving spots of light. Moving stimuli were much more effective in evoking oscillatory responses than were stationary stimuli (19 out of 20 cells). In no instance, using either stationary or moving stimuli, was the phase of the oscillatory response synchronized with the stimulus. These results demonstrate functional heterogeneity among cells within striate cortex based on their temporal firing patterns and provide evidence that the temporal pattern of oscillatory cellular activity is influenced by changes in stimulus properties.

Introduction

Much of what we see effortlessly in our daily lives involves the detection and recognition of visual objects and patterns which span many degrees over the visual field and which consist of a multitude of different feature combinations. Clearly, this capability of our visual system must involve the integration of information from different parts of the visual field and the establishment of relations between spatially distributed features (Marr, 1982; Treisman and Gelade, 1980; Treisman, 1986). Yet the picture of the central organization of the mammalian visual pathway which has emerged from over 30 years of research is one of topographic specificity, modularity, and functional localization (DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988; Zeki and Shipp, 1988). Cells at multiple levels in the visual pathway respond to a limited category of visual features within a restricted area of the visual field (Hubel and Wiesel, 1962, 1965). Thus, the evidence indicates that the vast majority of cells in the visual system view the world through a spatial and visual-feature aperture. How then, given this general picture of the central organization of the visual pathway, are the constellations of features which define objects in the real world combined and integrated into a perceptual whole?

It has been proposed on theoretical grounds that the selective temporal coordination of spatially distributed populations of cells within and between cortical areas could provide a mechanism for the segregation of figures from background and the segmentation of visual scenes (Malsburg, 1985; Malsburg and Schneider, 1986; Crick, 1984;

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Sejnowski, 1986; Malsburg and Singer, 1988; Damasio, 1989). Previously, we have presented evidence that cortical oscillatory responses provide a plausible functional substrate for the rapid temporal coordination of spatially distributed neuronal activity (Gray and Singer, 1987a,b, 1989; Gray *et al.*, 1989). We (Singer, 1990; Gray *et al.*, 1990) and others (Eckhorn *et al.*, 1988) have proposed that these interactions may underlie the integration of spatially distributed visual information. In our studies, in the cat, we have shown that a significant fraction of neurons in areas 17 and 18, but not in the lateral geniculate nucleus, exhibit an oscillatory firing pattern, at a frequency near 50 Hz, in response to their preferred stimuli. These neuronal responses are tightly correlated with an oscillatory local field potential recorded simultaneously through the same electrode (Gray and Singer, 1987a,b, 1989). When recorded in parallel at multiple sites the oscillatory responses synchronize in a stimulus-specific manner (Singer *et al.*, 1988; Gray *et al.*, 1989; Engel *et al.*, 1990; Eckhorn *et al.*, 1988). The magnitude of this functional interaction between separate cell groups was found to depend on their spatial separation, their similarity of orientation preference, the coherency of stimulus motion, and the spatial continuity of the stimulus. The results demonstrate that local subpopulations of cells in the visual cortex exhibit synchronous oscillatory responses which can transiently couple over relatively large areas of cortex in a stimulus-specific manner.

A number of issues remained unresolved from these studies, however. This report addresses three of those issues. First, the methods used in two of our previous studies did not enable us to characterize the receptive field properties and laminar positions of the cells which exhibit the oscillatory responses (Gray and Singer, 1989; Gray *et al.*, 1989). Only a fraction of the cells recorded, 47% and 66% respectively, exhibited oscillatory responses. In contrast, local field potential (LFP) recordings made in one of the studies (Gray and Singer, 1989), revealed stimulus-evoked increases in LFP activity in the range of 30–60 Hz in all of the recordings. These findings suggested that the oscillatory responses were confined to a subpopulation of cells in the cortex and that the LFP signal reflected activity in this subpopulation even in those cases when the underlying unit activity recorded from the same electrode showed no evidence of oscillations. In order to determine the nature of this subpopulation, we have made single unit recordings and classified the cells according to their receptive field type, laminar position and the occurrence of oscillatory responses.

A second issue not completely resolved by previous studies concerns the nature of the temporal coupling between the visual stimulus and the phase of the oscillatory responses. It has been demonstrated that the oscillatory responses evoked by optimal stimuli are not phase-locked to the stimulus presentation. Computation of the auto-correlogram using the shift predictor method (Gerstein and Perkel, 1969; Gray and Singer, 1989), and averaging of responses across trials (Eckhorn *et al.*, 1988), revealed no temporal synchronization between the stimulus and the oscillatory responses. Furthermore, this lack of stimulus synchronization was associated with a marked variability in the latency, duration and frequency of the oscillatory responses observed across trials (Gray and Singer, 1989). In order to evaluate this variability more precisely we have analysed oscillatory unit activity on a trial by trial basis to examine variations in these parameters. In addition, we have compared the temporal properties of the oscillatory responses to both moving and stationary stimuli, the latter providing a more precise temporal marker for the onset of the oscillation.

Finally, in order to resolve a third issue not fully addressed by previous studies we sought to investigate more thoroughly the stimulus-feature dependence of the oscillatory responses. This point was considered particularly important since any change in stimulus properties which influence the temporal behaviour of the oscillatory responses would also be expected to influence the temporal interaction of separate populations of cells. Previously it has been shown that binocular stimulation and stimulus velocity both influence the frequency and amplitude of oscillatory responses (Eckhorn *et al.*, 1988), while stimulus orientation has no effect on the response frequency (Gray and Singer, 1989). These studies, however, utilized field potential recordings which have a lower stimulus specificity. Therefore, as a starting point to more thoroughly examine these issues, we have investigated the influence of changing five different stimulus parameters on the temporal properties of oscillatory neuronal responses. These parameters include ocular dominance and binocular summation, orientation, velocity, length, and the influence of simultaneously presenting optimal and orthogonal stimuli.

The results reported here have been presented previously in abstract form (Engel *et al.*, 1989).

Materials and methods

The results of this study were obtained from 18 adult cats. The methods for surgical preparation and recording of single and multiple unit activity from the visual cortex were similar to those described previously (Gray and Singer, 1989; Gray *et al.*, 1989). For each experiment the cats were anaesthetized with an intramuscular injection of ketamine (15 mg/kg) and xylazine (5 mg/kg). A tracheotomy was performed and the animal was placed in the head holder of a stereotaxic instrument. The animal was artificially respired with a mixture of 70% O_2 and 30% N_2O, supplemented with 0.2–0.5% halothane. Neuromuscular blockade was achieved by a continuous i.v. infusion of hexacharbacholin bromide (0.4–0.6 mg/kg/h). End-tidal CO_2 and rectal temperature were monitored and maintained within the ranges of 3.0–4.0% and 37–38°C, respectively. The EKG was monitored and atropine (1%) and neosynephrine (5%) were applied to the eyes to dilate the pupils and retract the nictating membranes, respectively. Hard contact lenses, with appropriate correction for focus on a tangent screen at a distance 1.14 m from the cat, were placed over the eyes.

For single and multi-unit recording from the visual cortex two holes were drilled in the skull overlying area 17, one over each hemisphere. The dura was reflected and if necessary the pia removed. After placement of the recording electrodes overlying the cortical surface the cortex was covered with agar and the assembly sealed with bone wax. Extracellular recordings were made with both varnish-coated tungsten micro-electrodes as well as Teflon-coated platinum-iridium wires (25 μm dia.) (Mioche and Singer, 1989; Gray and Singer, 1989) mounted on an electronically controlled microdrive. The signals were amplified (10 k) and bandpass filtered (1–3 kHz). The resulting unit activity was detected with a window discriminator and digitized on-line at a frequency of 1 kHz.

The receptive fields of recorded neurons were first mapped using a hand-held lamp. The assessment of receptive field properties was similar to that employed by previous investigators (Hubel and Wiesel, 1962; Barlow *et al.*, 1967; Gilbert, 1977). The two principal criteria we employed for the distinction of cell types was the presence of either nonoverlapping (simple) or overlapping (complex) ON and OFF subfields, and the receptive field size. The category of complex cells was further subdivided into standard and special complex cells, the latter showing little or no length summation within the receptive field,

broad orientation tuning, equal preference for both eyes and little or no binocular summation (Palmer and Rosenquist, 1974; Gilbert, 1977; Hammond and Ahmed, 1985). Following the receptive field classification automated visual stimuli, consisting of moving light bars, were then projected onto a tangent screen with a computer controlled optical bench. On each trial the neuronal responses were recorded while the stimulus passed over the receptive field, first in one direction and then in the reverse direction, perpendicular to the orientation of the light bar. Each trial was 10 s in duration and was repeated 10 times. All units recorded had their receptive field locations within 15 degrees of the area centralis.

Several parameters of the visual stimuli were varied systematically in order to observe variations of the response properties: (i) stimulus orientation was varied by intervals of 22.5 degrees; (ii) stimulus velocity was varied by passing a moving light bar over the receptive field for a fixed distance and then varying the duration of the movement; (iii) ocular dominance and binocular summation were evaluated by aligning the receptive fields from the two eyes with a prism and then subsequently covering each eye separately; (iv) length summation was evaluated by changing the stimulus length in discrete intervals within and beyond the receptive field boundary; (v) the response to stationary light bars of optimal orientation flashed ON and OFF within the receptive field was also evaluated; (vi) the influence of combined stimulation with optimally and orthogonally orientated light bars was determined. A second light bar of equal luminance was presented, at an orientation orthogonal to the first, at the same velocity so that it passed through the receptive field centre at the same time as the optimal stimulus. Multiple comparisons were made by passing first the optimal stimulus alone, then the optimal and orthogonal stimulus together and then the orthogonal stimulus alone.

The amplitude- and time-dependent properties of the neuronal responses were evaluated by computing both the poststimulus-time histograms (PSTH) of the spike trains as well as their auto-correlation functions (ACF) (Perkel *et al.*, 1967). Tuning curves for stimulus orientation, velocity and length were computed by either counting the number of spikes within a 1 s time window centred at the peak of the response, or measuring the maximum firing rate of the response. Both calculations were made for each direction of stimulus movement. The response amplitudes were normalized to the peak response recorded during assessment of a particular tuning curve and expressed as a percentage of the maximum response. A similar procedure was applied to changes in response amplitude which occurred when stimulating one or both eyes and when co-stimulating the receptive fields with orthogonally orientated light bars.

In order to evaluate the temporal properties of the oscillatory responses we developed a method to quantify the occurrence and magnitude of rhythmic responses revealed by the auto-correlograms. Each ACF was digitally low-pass filtered using two passes of a 1:1:1 smoothing routine. The latency and amplitude of the first trough and peak in the ACF were then computed. The reciprocal of the latency to the first peak was defined as the frequency of the oscillatory response, and the amplitude from the first trough to the first peak was defined as the modulation amplitude. We also computed the offset amplitude of the ACF by taking the average of the number of spikes in the bins ranging from 5 to 60 ms time lag. By calculating the ratio of the modulation amplitude with respect to the offset amplitude we obtained a measure of the oscillatory modulation amplitude normalized for variations in the total number of spikes. The coefficients obtained from these analyses were utilized to determine the occurrence of oscillatory responses, as well as their frequency and modulation amplitude. Responses were accepted as oscillatory when the ACF had at least one secondary peak and when the modulation amplitude of the waveform exceeded 10% of the amplitude of the shift predictor. For responses exhibiting a clear rhythmicity (i.e. with a modulation amplitude of more than 20% of the shift predictor amplitude) we evaluated the changes in modulation amplitude and frequency as a function of stimulus properties.

Results

Receptive field properties

The receptive field dependence of oscillatory responses was examined in a total of 133 single cells. The results of this analysis are shown in Table 1. In general we found a clear difference in the temporal pattern of firing between simple and complex cells. The vast majority of simple cells showed little or no evidence of oscillatory activity in response to their preferred stimulus. The firing pattern of these cells, as revealed by the ACF, typically showed a refractory period of 2–5 ms followed by a relatively flat distribution. The range of inter-spike intervals showed broad variation with no clear evidence of periodicity. Figure 1 illustrates the response of a typical nonoscillatory simple cell to monocular stimulation. The spike train, examined on selected trials (Fig. 1C,D), showed no evidence of periodicity when displayed at high or low temporal resolution. This was confirmed by the ACF (Fig. 1B) which showed a brief, 2–3 ms, refractory period followed by a flat distribution.

Seven of the simple cells we recorded from did show evidence of an oscillatory firing pattern. The responses of these cells were similar to those observed in the other simple cells except for their tendency to fire rhythmically and in bursts. In this respect their firing pattern looked very similar to that of the rhythmically firing complex cells. In fact, the frequency of oscillation of the simple and complex cells was identical (Table 1). An example of the temporal pattern of activity of an oscillatory simple cell is shown in Figure 2. The cell fired strongly in response to both directions of stimulus movement. The auto-correlogram computed for each direction shows evidence of a weak periodicity in the spike train at an interval of 20 ms. Closer examination of the spike trains on selected trials, however, revealed brief periods of clear oscillatory activity. The intervals between cycles ranged in duration from 15 to 30 ms and on each cycle of the oscillation the cell fired 1–5 spikes, a property characteristic of bursting behaviour (McCormick *et al.*, 1985). Thus, these cells were capable of firing at instantaneous rates as high as 200–400 Hz.

In contrast to the typical temporal behaviour of simple cells a large fraction of the complex cells (42%) exhibited an oscillatory firing pattern. This propensity for rhythmic firing was differentially distributed between the standard and special complex cell types, the standard

TABLE 1. Percentage of cells in each receptive field category which exhibit oscillatory firing patterns in response to their preferred stimuli. The mean frequency and modulation amplitude is displayed for those cells in each category which show oscillatory responses

	Per cent	Freq (Hz)	Mod amp
Simple (n = 7)	7/60 (%12)	47±8	0.24±0.07
Std complex (n = 30)	30/54 (%56)	47±8	0.26±0.12
Sp complex (n = 2)	2/29 (%11)	49	0.21

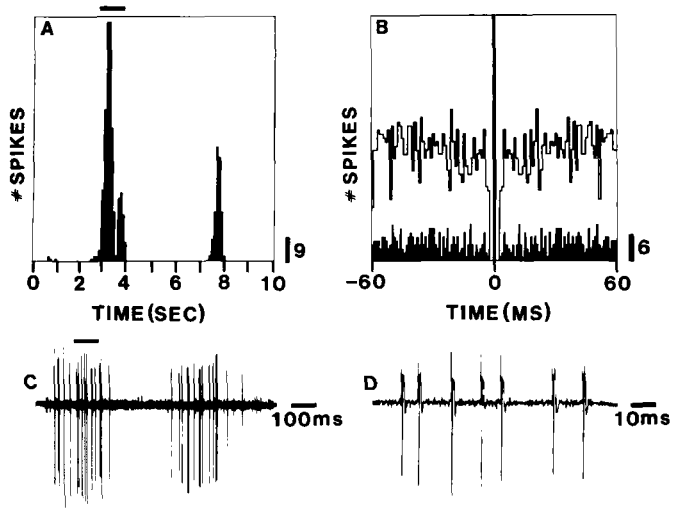

FIG. 1. The firing pattern of a typical simple cell shows no evidence of oscillations. (A) Post-stimulus-time histogram of the neuronal spike train recorded in response to 10 presentations of an optimally orientated light bar. (B) Auto-correlograms of the same spike train shown in A. Unfilled and filled bars indicate the first and second direction of stimulus movement, respectively. (C) Plot of the spike train recorded during the response to a single presentation of the light bar at the preferred direction of movement. The epoch of data sampled from this plot is shown by the dark bar overlying the PSTH in A. (D) High temporal resolution display of a portion of the same spike train shown in C. The epoch of data sampled for display is shown by the dark bar in C. The conventions used for the display of data in this figure are the same for Figures 2–4.

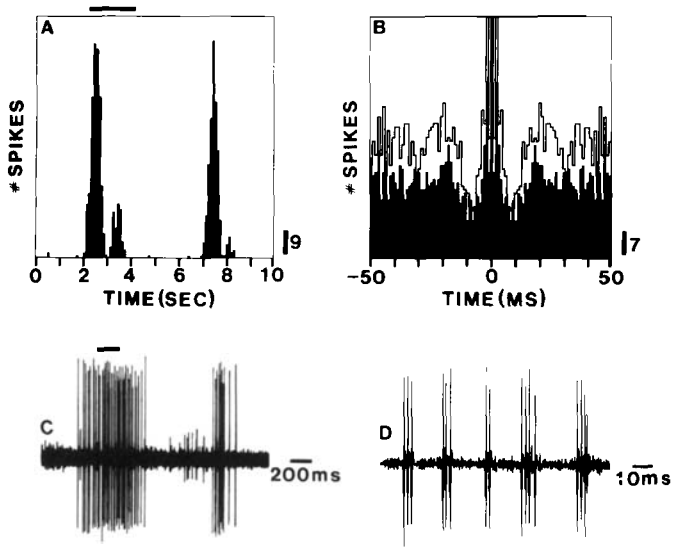

FIG. 2. The firing pattern of an oscillatory simple cell. (A) Post-stimulus-time histogram of the neuronal spike train recorded over 10 trials. (B) Auto-correlograms. (C) Plot of the spike train recorded during a single presentation to the first direction of stimulus movement. (D) High resolution plot of the same data shown in C.

complex cells showing a much higher tendency to oscillate (Table 1). Again, the oscillatory pattern consisted of bursts of spikes in which the inter-burst intervals ranged from 15 to 30 ms. An example of an oscillatory standard complex cell is shown in Figure 3.

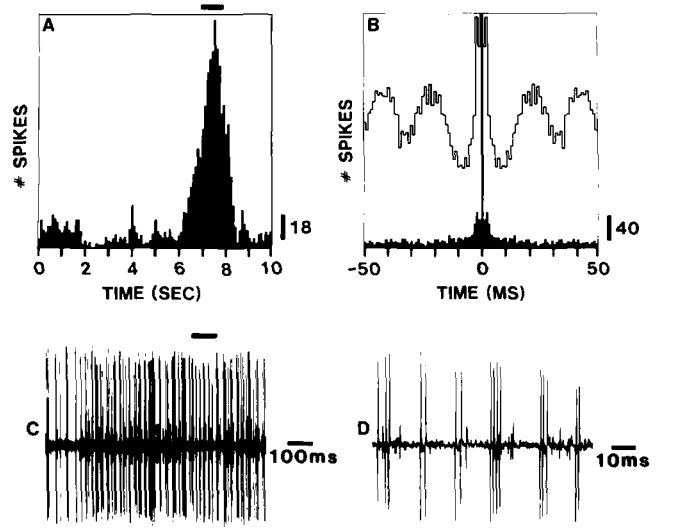

FIG. 3. The firing pattern of an oscillatory standard-complex cell. (A) Post-stimulus-time histogram of the neuronal spike train recorded over 10 trials. The response is selective for the second direction of stimulus movement. (B) Auto-correlograms. Filled and unfilled bars display the correlograms computed for the first and second direction of stimulus movement respectively. (C) Plot of the spike train recorded during a single presentation to the second direction of stimulus movement. (D) High resolution plot of the same data shown in C.

Although in our sample over 50% of the standard complex cells showed evidence of oscillatory behaviour, there were many clear and unambiguous examples of standard complex cells which did not oscillate. Figure 4 shows one such example. In these cases the firing pattern was somewhat similar to that of the majority of simple cells. The cells fired at rates as high as 200 Hz, but showed no tendency for bursting. Spikes usually occurred in isolation having a refractory period of 3–8 ms. Moreover, the interspike intervals were randomly distributed, yielding a flat auto-correlogram over a range of intervals extending to 60 ms. This temporal firing behaviour was also typical of special complex cells. We did, however, observe oscillatory activity in two special complex cells. As shown in Table 1, the frequency and modulation amplitude of the oscillatory responses did not differ across cell types.

Of the cells exhibiting oscillatory responses, 21 were localized, using histological reconstruction, to a particular layer within area 17 (Table 2). Eighteen of these cells had standard complex receptive fields and three had simple receptive fields. Two of the simple cells were located in layer 6 and one in layer 4. Although we recorded from cells in all layers there was a relative paucity of cells in layer 4 which showed oscillatory responses, a finding which is consistent with the known laminar distribution of standard complex cells (Gilbert, 1977).

Feature dependence of oscillatory responses

One of the principal aims of this study was to assess the influence of different stimulus parameters on the temporal properties of oscillatory neuronal responses. In order to facilitate data collection we utilized recordings of both single cells as well as multiunit recordings in which more than one cell was well resolved. However, to avoid ambiguity, we chose only those recordings for analysis which exhibited a clear oscillatory modulation in their auto-correlograms (i.e. the ratio of modulation amplitude to offset amplitude exceeded 0.2). This enabled

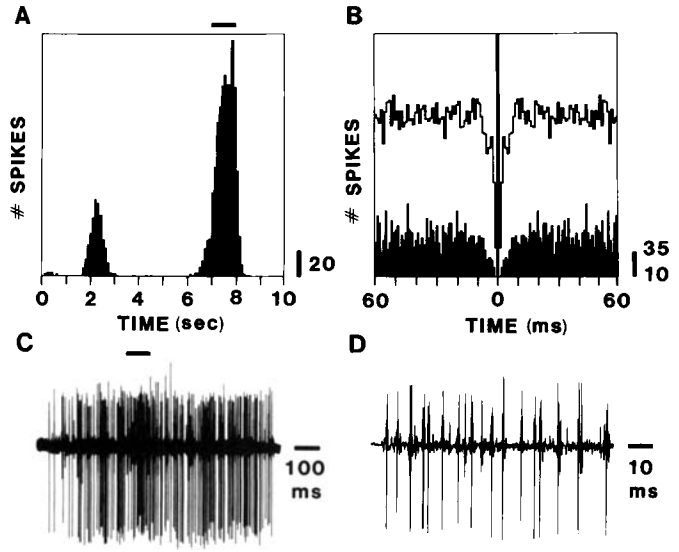

FIG. 4. The firing pattern of a nonoscillatory standard-complex cell. (A) Post-stimulus-time histogram of the neuronal spike train recorded over 10 trials. The response shows a preference for the second direction of stimulus movement. (B) Auto-correlograms. Filled and unfilled bars display the correlograms computed for the first and second direction of stimulus movement, respectively. (C) Plot of the spike train recorded during a single presentation to the second direction of stimulus movement. (D) High resolution plot of the same data shown in C.

TABLE 2. The laminar distribution of cells exhibiting an oscillatory firing pattern in response to their preferred stimulus as a fraction of the total number of cells identified for each layer

Layer	2+3	4	5	6
No. cells	8/20	2/15	4/9	7/27

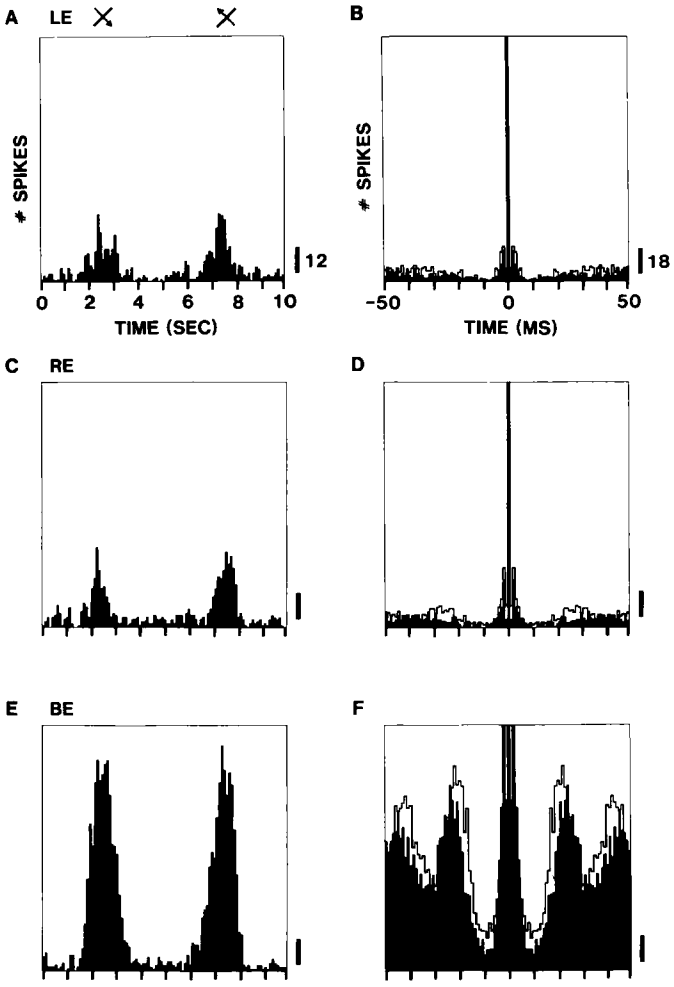

FIG. 5. Binocular stimulation enhances oscillatory responses. (A,B) Post-stimulus-time histogram and auto-correlograms, respectively, recorded in response to stimulation through the left eye. (C,D) and (E,F) show the corresponding PSTHs and auto-correlograms to stimulation through the right eye and both eyes, respectively. In each plot of the auto-correlograms the filled and unfilled bars are for the first and second directions of stimulus movement, respectively.

us to clearly discriminate changes in modulation amplitude and frequency as a function of changing stimulus conditions.

Interocular interactions

In the majority of cells the most effective stimulus for evoking oscillatory responses was a moving light bar of optimal orientation, direction, velocity and length presented to both eyes aligned with prisms (Fig. 5). In 26 recordings we determined the influence of binocular vs monocular stimulation on the oscillatory responses. After acquiring the data under three conditions (i.e. stimulation through left eye, right eye and both eyes) we evaluated the receptive field alignment in each recording by comparing the latencies, observed in the PSTHs, of each of the monocular responses. Using nearly complete temporal overlap of the two monocular responses as a criterion for alignment, 16 of our recordings showed good receptive field alignment. The remaining 10 recordings were not well aligned. These two categories of cells were analysed separately. All 26 recordings were evaluated for ocular dominance (5 point rating scale) and binocular summation or suppression.

In the recordings showing good temporal overlap of the two monocular responses 10 out of 16 cases exhibited binocular summation (i.e. the response amplitude to binocular stimulation exceeded the response to either eye alone). The cells in each of these 10 cases were binocular, with their responses being classified in categories 2–4 on a 5-point ocular dominance scale. In nine of these 10 recordings the modulation amplitude of the oscillatory response to binocular stimulation was greater than in either monocular condition alone (Table 3A). And in five of the 10 cases the monocular responses showed little or no oscillatory modulation (compare B and D to F in Fig. 5). The oscillation frequencies of the monocular responses were slightly, but insignificantly, lower than those of the binocular responses.

In six of the recordings having well aligned receptive fields we saw no evidence of binocular summation and in these cells there were also no significant differences in the modulation amplitude or frequency between binocular and monocular oscillatory responses (Table 3B). In one case, where we observed a slight binocular suppression, the modulation amplitude of the ACF was reduced with binocular stimulation compared to either of the monocular responses.

In the 10 cells showing a poor alignment of the receptive fields ocularity was more strongly biased towards one eye than in the other

TABLE 3. The dependence of oscillatory response properties on stimulus ocularity. BE, DE and NE are for both, dominant and nondominant eyes respectively

A. Well aligned with binocular summation (n = 10)

	Amplitude			Mod amplitude			Frequency		
	BE	DE	NE	BE	DE	NE	BE	DE	NE
Mean	1	0.58	0.47	0.31	0.15[a]	0.15[b]	43	39	41
SD				0.10	0.12	0.16	7	10	12

[a]BE significantly greater than DE at $P < 0.003$ *U*-test
[b] BE significantly greater than NE at $P < 0.009$ *U*-test

B. Well aligned without binocular summation (n = 6)

	BE	DE	NE	BE	DE	NE	BE	DE	NE
Mean	1	0.98	0.78	0.25	0.24	0.24	49	49	49
SD				0.08	0.11	0.15	5	8	11

No significant differences

C. Poorly aligned (n = 10)

	BE	DE	NE	BE	DE	NE	BE	DE	NE
Mean	0.91	0.93	0.60	0.26[a]	0.22[b]	0.12	46	45	50
SD				0.08	0.10	0.11	5	9	4

[a]BE significantly greater than NE at $P < 0.009$ *U*-test.
[b]DE significantly greater than NE at $P < 0.014$ *U*-test

TABLE 4. The influence of moving and stationary stimuli on the properties of oscillatory responses

	Moving (n = 20)		Stationary (n = 13)	
	Mod amp	Freq	Mod amp	Freq
Mean	0.233	55	0.132[a]	49
SD	0.060	11	0.036	12

[a]Stationary significantly lower than moving at $P < 0.00003$ *U*-test

two categories. In these 10 cases the oscillatory modulation of the responses to binocular and dominant eye stimulation were equal and both exceeded that observed in response to the non-dominant eye (Table 3C).

Stationary versus moving stimuli

It is well established that moving stimuli are generally more effective at driving cortical neurons, than are stationary stimuli flashed on and off within the receptive field (Hubel and Wiesel, 1962; Movshon, 1975; Emerson and Gerstein, 1977; Goodwin and Henry, 1978). Neurons exhibiting oscillatory responses show no exception to this rule. We compared the responses to stationary and moving stimuli of optimal orientation, length and ocularity in 20 recordings showing robust oscillatory behaviour to moving stimuli (Table 4). In seven of the recordings the responses to stationary flashed stimuli showed no evidence of rhythmic firing. In 12 out of the 13 remaining cases the oscillatory modulation was lower in response to the stationary stimulus than that observed to the moving stimulus. Figure 6 shows an example of a standard complex cell in which the temporal properties of the responses clearly differ between the moving and stationary stimulus conditions. For the stationary condition the optimal stimulus was positioned in the centre of the receptive field and then turned ON and OFF at latencies of 3 and 7 s with respect to the onset of each trial

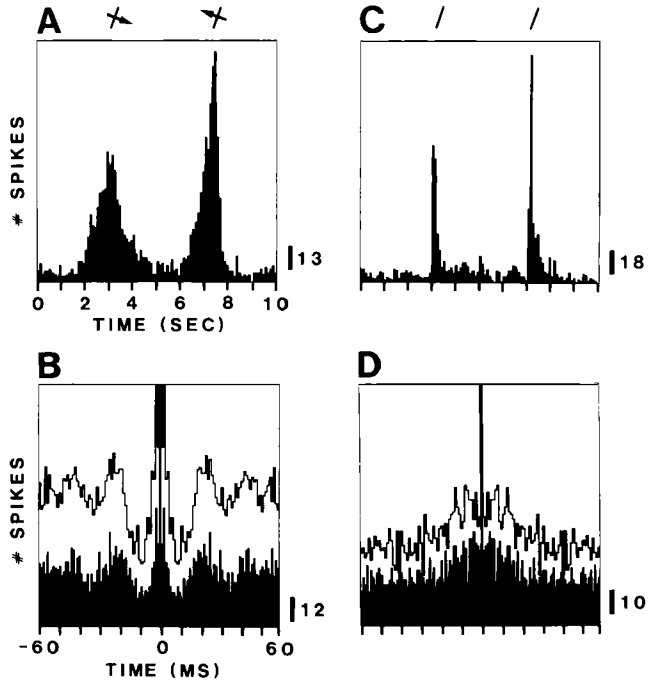

FIG. 6. Oscillatory neuronal activity occurs preferentially in response to moving rather than stationary stimuli. A,C and B,D show post-stimulus-time histograms and auto-correlograms, respectively, computed from the responses to moving (A,B) and stationary (C,D) stimuli at the optimal orientation. The stationary light bars were centred within the receptive field and flashed on (3 s) and off (7 s). The unfilled bars in the auto-correlograms display the data for the second direction of stimulus movement (B) and for the offset of the light bar (D).

TABLE 5. The influence of stimulus orientation on the frequency and modulation amplitude of oscillatory responses

Angle	±67	−45	−22	0	22	45
Frequency						
Mean	52	52	52	53	52	52
SD	7	7	6	5	5	7
Modulation amplitude						
Mean	0.15[a]	0.18[b]	0.29	0.37	0.30	0.18[c]
SD	0.08	0.10	0.19	0.14	0.15	0.13

[a]±67 significantly lower than 0 at $P < 0.003$ *t*-test
[b]−45 significantly lower than 0 at $P < 0.0004$ *U*-test
[c]+45 significantly lower than 0 at $P < 0.0004$ *U*-test

(Fig. 6C). The auto-correlations of the ON and OFF responses show little or no oscillatory modulation and the temporal properties of the responses are markedly different.

Orientation

In 18 recordings we evaluated the influence of changes in stimulus orientation on the frequency and modulation amplitude of the oscillatory responses (Table 5). Because of variations in orientation tuning the range of orientations examined varied from one recording to the next. In six cases the tuning was such that the responses could only be evaluated for orientations of ±22.5 degrees from optimal. In nine cases this range could be extended to ±45 degrees from optimal and in the three remaining cases we were able to evaluate orientations of ±67.5 degrees from optimal. In general, oscillatory responses could be easily detected at nonoptimal stimulus orientations.

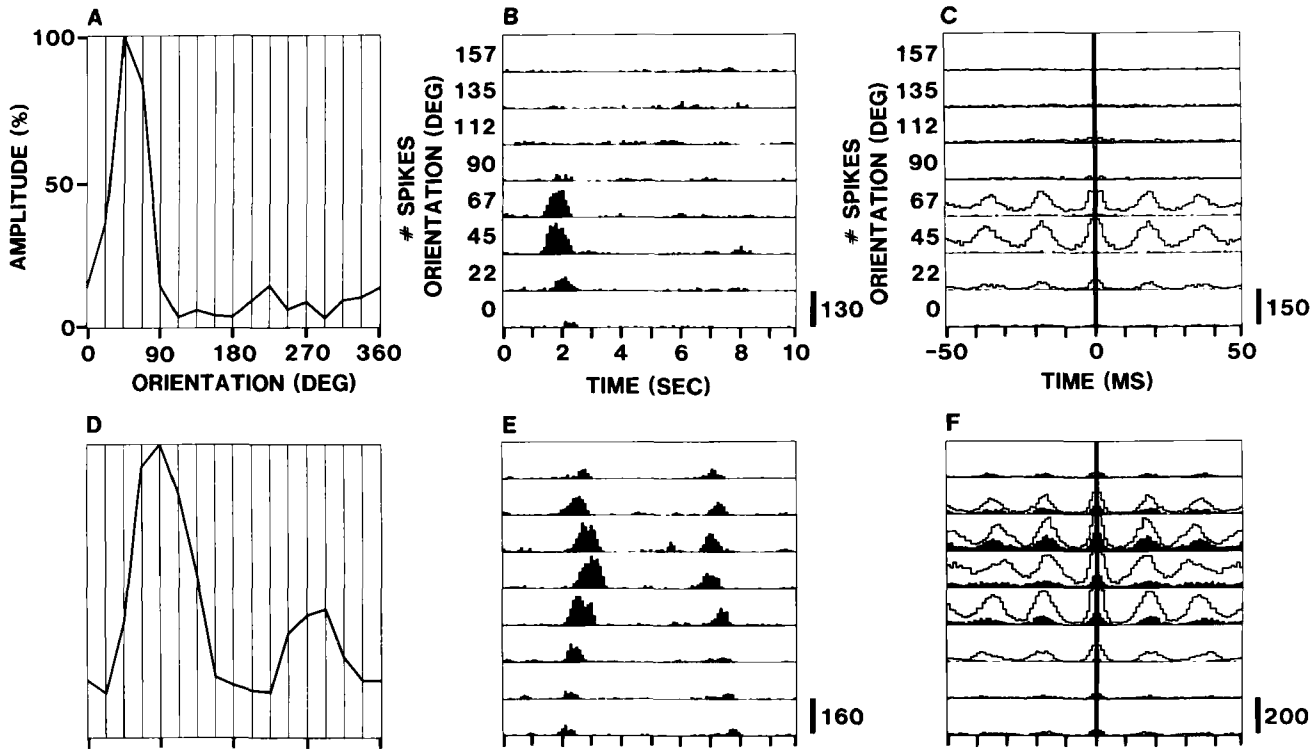

FIG. 7. Oscillatory response frequency does not change as a function of stimulus orientation. (A–C) Orientation tuning curve, post-stimulus-time histograms, and corresponding auto-correlograms computed for a cell tightly tuned for orientation and direction. (D–F) A similar display as that shown in A, B and C, for a cell more broadly tuned for orientation and direction. In each example the unfilled bars of the auto-correlograms display the first direction of stimulus movement.

The principal effect on oscillatory responses of changing stimulus orientation away from that preferred by the cells was a reduction of the oscillatory modulation amplitude (Table 5). This effect occurred despite little or no change in oscillation frequency (Table 5). Figure 7 exemplifies these results and shows the responses recorded from two different cells in which the orientation tuning differs. In one case (A,B,C) oscillatory responses occurred at orientations of ± 22.5 degrees from optimal which were of sufficient quality to evaluate their frequency and modulation amplitude. In D, E and F the oscillatory responses occur over a broader range of orientations so that even at orientations of ± 67.5 degrees from optimal a discernible oscillatory response can be seen. In neither case does the frequency at suboptimal orientations differ from that at the optimal orientation by more than ± 3 Hz. This finding was characteristic of the sample as a whole. In 13 out of the 18 recordings the frequency of the oscillatory responses at the suboptimal orientations did not differ from the frequency to the optimal stimulus by more than ± 4 Hz. In those cases in which the frequency differed by 5 Hz or more we found an equal proportion (3:3) of frequency increases and decreases.

Velocity

We evaluated the influence of changes in stimulus velocity on the temporal properties of oscillatory responses from 11 recordings. In each case a moving light bar of optimal orientation was passed over the receptive field, in both directions perpendicular to the axis of orientation, for a fixed distance ranging from 4 to 8 degrees of visual angle. Stimulus velocity was varied by changing the duration during which the stimulus moved the specified distance. The velocities tested ranged from 0.5 to 62°/s. In each case, however, we attempted to use a range of stimulus velocities which evoked responses of at least 50% of the maximum amplitude, when using peak firing rate (evaluated with a resolution of 100 ms; cf. Fig. 8) as the measure of response amplitude.

In general we found a strong correlation between stimulus velocity and the occurrence, frequency and modulation amplitude of oscillatory responses. In ten out of 11 cases the oscillatory frequency increased monotonically with stimuli velocity. However, due to differences in frequency variance (F-test) the sample as a whole did not significantly reflect this effect (Table 6). There was no evidence for oscillatory responses in any of the 11 recordings when the stimulus velocity exceeded 13°/s. And the stimulus velocities which evoked the maximum firing rates of the neurons were greater in ten out of 11 cases than those which evoked well resolved oscillatory responses. Using the maximum firing rate as a measure of velocity preference we found that the average preferred velocity of our sample of cells was 8.8 ± 5°/s. At this velocity only four out of the 11 recordings showed an oscillatory modulation in their auto-correlograms. In contrast, when we used the maximum modulation amplitude of the oscillatory responses as a criterion for velocity preference the average preferred velocity was 2 ± 0.7°/s ($n = 11$). Thus, the range of stimulus velocities which evoke oscillatory responses is significantly lower than that which evokes a maximum rate of firing.

Within this lower range of velocities (0.5–12°/s), which evoke oscillatory activity, the frequency of the oscillation increased as a function of the stimulus velocity while the modulation amplitude first increased and then decreased (Table 6). Figure 8 illustrates two examples of this effect. The modulation amplitude first increases and then decreases as stimulus velocities become greater. This effect is paralleled by a monotonic increase in response frequency until, at

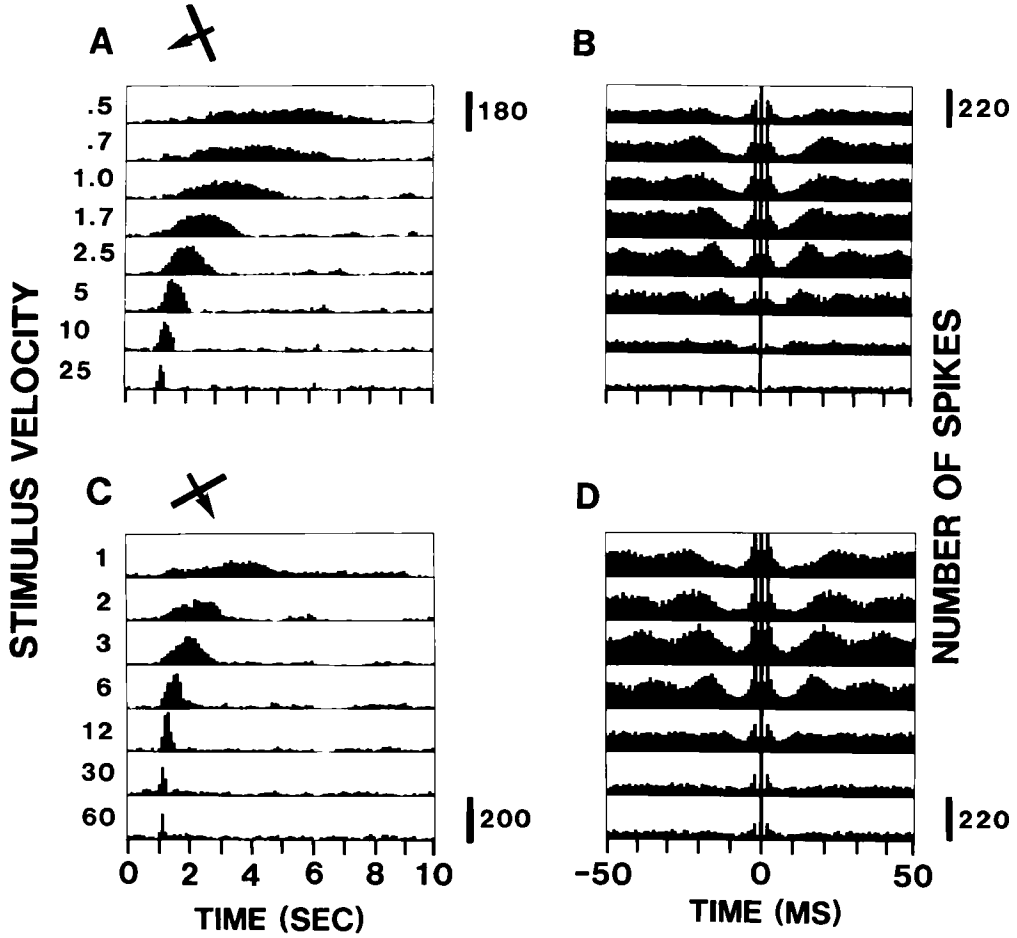

FIG. 8. Oscillatory response frequency and modulation amplitude vary as a function of stimuli velocity. A,C and B,D show the post-stimulus-time histograms and auto-correlograms, respectively, computed for two direction selective cells (A,B) and (C,D), over a wide range of stimulus velocities. The velocity values are shown to the left of A and C.

velocities greater than 10°/s, little or no modulation can be seen in the auto-correlograms. This latter effect occurs even though the neurons are responding at or near their maximum firing rate. The example shown in Figure 8A,B shows a particularly broad range of oscillation frequencies which could be discerned from the auto-correlograms. In this case the frequencies ranged from 48 to 83 Hz.

Length

We investigated, in 15 multiunit recordings, the influence of stimulus length on the oscillatory responses evoked by moving light bars of optimal orientation and velocity. The lengths of the receptive fields parallel to the axis of optimal orientation ranged from 3 to 6 degrees. Due to the large variability of receptive size we examined the properties of the oscillatory responses over a broad range of stimulus lengths (0.5 – 12 degrees) and expressed the results as a function of stimulus length irrespective of receptive field dimensions. In four of the recordings comparisons were made only between responses to stimuli matched to the length of the receptive field with responses evoked by light bars extending well beyond the boundary of the receptive field.

The results of this analysis are shown in Table 7. Four of the recordings exhibited end inhibition in which the responses to long bars were suppressed from 20 to 40% of the maximum response. We excluded these data from the tabulated results. In the remaining cases we found that as stimulus length was increased the oscillatory modulation and response amplitude increased in parallel. In six out of 11 cases we observed no oscillatory modulation in response to small light bars, 0.5 degrees square. Extension of the stimulus length well beyond the boundaries of the receptive field (7 – 12 degrees) resulted in only weak additional increases in oscillatory modulation amplitude (10 out of 11 cases). In two of the four cases showing end inhibition the oscillatory modulation decreased when stimulus length was increased beyond the optimal. In general the oscillatory response frequency did not vary as a function of stimulus length (Table 7).

TABLE 6. The influence of stimulus velocity on the frequency and modulation amplitude of oscillatory responses

Velocity (°/s)	0 – 1	1 – 2	2 – 3	3 – 6	> 6
Frequency					
Mean	48	45	51	55	57
SD	4	7	9	10	15
Modulation amplitude					
Mean	0.27[a]	0.34	0.37	0.32	0.25[b]
SD	0.06	0.11	0.06	0.08	0.04

[a] 0 – 1 significantly lower than 2 – 3 at $P < 0.01$ *t*-test
[b] > 6 significantly lower than 2 – 3 at $P < 0.005$ *t*-test

TABLE 7. The influence of stimulus length on the frequency, modulation amplitude and response amplitude of oscillatory responses (n = 11)

Length (deg)	0–1	1–2	2–4	4–7	7–12
Frequency					
Mean	54	50	48	51	52
SD	7	11	14	10	9
Modulation amplitude					
Mean	0.13[a]	0.17[b]	0.18[c]	0.31	0.36
SD	0.03	0.07	0.06	0.10	0.09
Response amplitude					
Mean	0.3[d]	0.59[e]	0.61[f]	0.85	0.94
SD	0.2	0.25	0.29	0.17	0.09

[a]0–1 significantly lower than 7–12 at $P < 0.00001$ *t*-test
[b]1–2 significantly lower than 7–12 at $P < 0.0002$ *t*-test
[c]2–4 significantly lower than 7–12 at $P < 0.0008$ *t*-test
[d]0–1 significantly lower than 7–12 at $P < 0.00001$ *t*-test
[e]1–2 significantly lower than 7–12 at $P < 0.003$ *t*-test
[f]2–4 significantly lower than 7–12 at $P < 0.02$ *t*-test

Conflicting stimuli

It has been argued on theoretical grounds that combinations of stimuli, such as two light bars of different orientation, should have a confounding effect on neuronal responses (Ballard *et al.*, 1983). Moreover, a large body of evidence has accumulated, indicating that nonoptimally orientated stimuli have an inhibitory influence on neuron responses to the preferred stimulus (Ferster and Koch, 1987; Hata *et al.*, 1988). These influences could in turn alter the temporal firing patterns of the neurons under study. Thus, we sought to determine the influence of simultaneously presenting two stimuli of orthogonal orientations on the temporal properties of the oscillatory responses.

After mapping the receptive field for a cell showing an oscillatory response we quantitatively determined the cell's orientation preference. We then compared the response of the cell when stimulated at its preferred orientation to its response when activated by both the optimally and orthogonally oriented stimuli of the same luminance. When possible these comparisons were made several times.

We examined a total of 21 cells which gave robust oscillatory responses to their preferred stimulus. In 16 of the 21 cases the combined presentation of optimally and orthogonally orientated stimuli caused a reduction of the oscillatory modulation of the response as compared to the optimal stimulus alone (Table 8). This reduction in response rhythmicity ranged from complete abolition to only slight suppression. Combined with this general reduction in response rhythmicity the two stimuli presented together also caused a reduction in the response amplitude (18 out of 21) as compared to the optimal stimulus alone. In 14 cases both response amplitude and oscillatory modulation amplitude were reduced. In four cases the response rhythmicity was unchanged and in one case it was enhanced by the orthogonal stimulus. Figure 9 illustrates a case in which the orthogonal stimulus caused a nearly complete suppression of the oscillatory modulation of the ACF even though the response amplitude remained unchanged. Although we observed a reduction in the oscillatory frequency of more than 3 Hz in seven out of 21 cases the frequency of the oscillatory responses was generally the same in the two conditions (Table 8).

Response variability

It has been demonstrated previously, with field potential recordings, that the phase of oscillatory responses is not synchronized to the evoking stimulus (Gray and Singer, 1987a,b, 1989; Eckhorn *et al.*, 1988). In order to confirm and extend these findings we have examined oscillatory

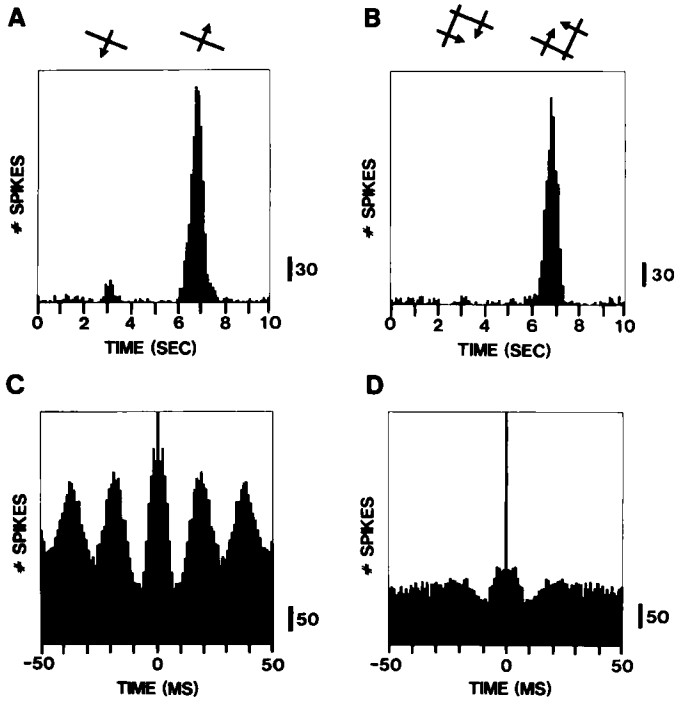

FIG. 9. The simultaneous presentation of stimuli having optimal and orthogonal orientations reduces the modulation amplitude of oscillatory responses to optimal stimuli presented alone. A,B and C,D show post-stimulus-time histograms and auto-correlograms, respectively, computed from responses recorded during presentation of an optimal stimulus alone (A,C) and when combined with an orthogonal stimulus (B,D).

TABLE 8. Comparison between the influences of optimally orientated stimuli and the combined presentation of optimally and orthogonally orientated stimuli on the frequency and modulation amplitude of oscillatory responses

	Optimal		Optimal + orthogonal	
	Mod	Freq	Mod	Freq
Mean	0.41	48	0.29[a]	46
SD	0.19	7	0.16	5

[a]Conflicting condition significantly lower than optimal at $P<0.004$ *U*-test.

unit responses to both moving and stationary stimuli. We selected 12 recordings of both single and multiunit activity in which the oscillatory modulation of the ACF exceeded 0.4. The temporal firing patterns of these cells were such that stimulus-evoked oscillations could be easily seen in the raw spike trains. Thus, we could inspect the raw data, as well as compute auto-correlograms on individual trials. In each of the 12 recordings the oscillatory responses, observable in the spike trains, were not synchronized across trials. This general impression was supported by the lack of oscillatory modulation in the shift predictor of the auto-correlogram. In addition, when we examined the slow envelope of the responses, as seen in the spike trains, the exact onset and duration of the responses also varied from trial to trial. Further confirmation of these findings was obtained by computing the auto-correlogram on each trial and comparing the distributions across trials. This approach revealed that the modulation amplitude and the frequency of the oscillatory responses also varied from trial to trial (Fig. 10).

In those recordings in which the response to a stationary stimulus

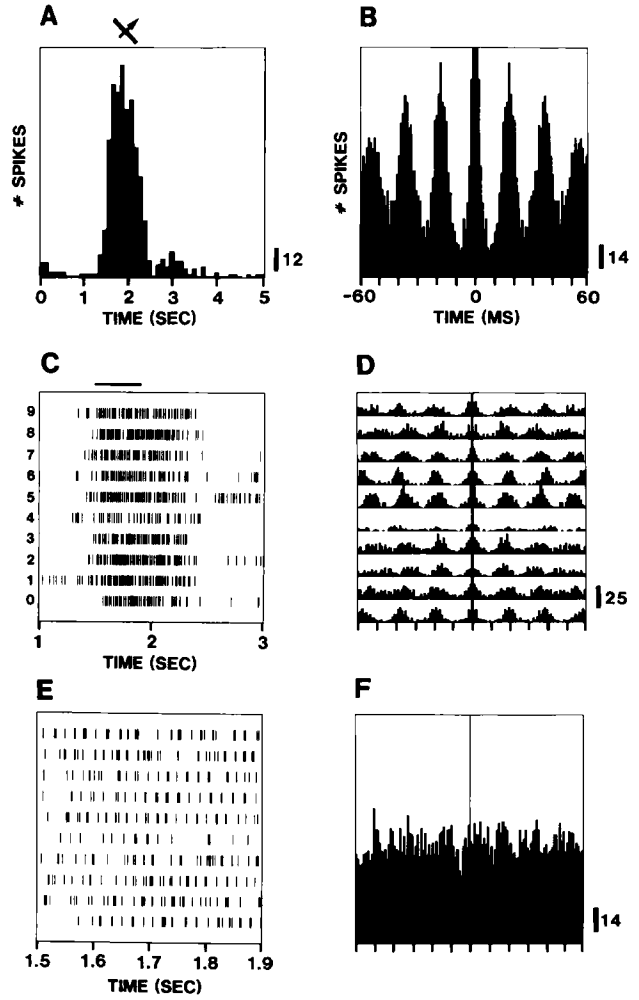

FIG. 10. The onset latency, frequency, amplitude and temporal phase of oscillatory responses are not time-locked to the stimulus presentation. (A) Post-stimulus-time histogram of a multiunit recording computed from the response to the preferred direction of stimulus movement. (B) Auto-correlogram computed from the same spike train data shown in A. (C) Raw spike trains displayed for each of the 10 trials recorded between the second and third seconds of the stimulus presentation. (D) Auto-correlograms computed from the spike trains recorded during each of the 10 stimulus presentations. (E) High resolution display of the spike trains recorded on each of the 10 trials shown in C. The epoch chosen for display is indicated by the time axis as well as the dark bar overlying the plot in C. (F) Re-computation of the auto-correlogram after shuffling the trial sequence by one stimuli period.

continued to exhibit an oscillation, we sought to determine if the oscillation was phase locked to the stimulus onset or offset. In general we found that there was a high degree of temporal variability for the onset of an oscillatory response to a stationary stimulus. Again, the shift predictor of the auto-correlogram revealed no synchronization of the oscillations across trials and thus no precise phase-locking to the stimulus onset.

Discussion

Single cell properties

The present results confirm and extend our knowledge of the properties of oscillatory neuronal responses in the striate cortex of lightly anaesthetized cats in three general categories (Gray and Singer, 1989; Gray *et al.*, 1989; Engel *et al.*, 1990). First, the data demonstrate that oscillatory neuronal activity can be easily detected in the responses of single cells to specific visual stimulation. The firing patterns of these cells, which we term an oscillation, typically consists of bursts of action potential lasting 3–7 ms at instantaneous rates as high as 200–400 Hz which occur at regular intervals ranging from 16 to 30 ms. The nonoscillatory cells show little evidence of such high instantaneous firing rates or rhythmical patterns. The occurrence of this oscillatory firing pattern is limited primarily, but not exclusively, to a subpopulation of cells having standard complex receptive field properties. Oscillatory responses also occur among cells having simple and special complex receptive fields, but with a lower probability than that observed for the standard complex cells. The cells exhibiting oscillatory responses are distributed primarily in supra- (2+3) and infragranular (5+6) layers, a finding consistent with the known laminar distribution of standard complex and simple cells (Hubel and Wiesel, 1962; Gilbert, 1977; Martin and Whitteridge, 1984). Thus, the data are consistent with the notion of functional heterogeneity among cell types based on temporal firing patterns (McCormick *et al.*, 1985).

Although the present results support this interpretation we cannot exclude three potential sources of error which may have led to an incorrect estimate of the percentage of cells participating in the oscillatory responses. First, under different experimental conditions, such as attentive behaviour (Freeman, 1975; Raether *et al.*, 1989), the oscillatory cells may act to entrain additional populations of cells into temporally coherent activity (Connors, 1984; Chagnac-Amitai and Connors, 1989). Second, the technique of evaluating rhythmic firing by analysis of the average auto-correlogram of the spike train may have led to an underestimate of the percentage of oscillatory cells. The single trial analysis of oscillatory responses, carried out in this and a previous study (Gray and Singer, 1989), has demonstrated that the oscillation frequency and amplitude can vary between and within responses on a time scale of tens of milliseconds. Such variable behaviour is not well characterized by a measurement like the auto-correlation function (Freeman, 1975). This intra- and inter-trial variability leads to smoothing of the auto-correlograms and often the complete absence of detectable rhythmicity when observing the average auto-correlogram. Third, the firing patterns of the oscillatory and nonoscillatory cells may be related statistically. Several lines of evidence support this conjecture. Cross-correlation studies (Toyama *et al.*, 1981a,b; Michalski *et al.*, 1983; Tsó *et al.*, 1986; Schwarz and Bolz, 1989) have demonstrated widespread correlated interactions between simple and complex cells in similar as well as different layers of the cortex. There is substantial evidence from studies of other brain regions, as well as network simulations, that the spike trains of neurons, which often show no evidence of rhythmic firing, can nonetheless exhibit a close correlation to the coherently active population of cells in which they are embedded (Freeman, 1975; Gray and Skinner, 1988; Gray and Singer, 1989; Traub *et al.*, 1989; Alonso and Llinas, 1989; Sporns *et al.*, 1989). Therefore, it is likely that the results presented here may actually reflect an underestimate of the proportion of cells which participate in synchronous oscillations.

Given this caveat, there are nonetheless many examples of cells which fire at high rates and show no evidence of regular rhythmic oscillations, even after close examination of the spike trains. This suggests that the cells participating in the synchronous oscillations may be limited to a subpopulation. Our finding that oscillatory responses occur primarily in standard complex cells in supra- and infra-granular layers as opposed

to special complex and simple cells is also consistent with this notion. These three cell types differ in their functional receptive field properties (Hubel and Wiesel, 1962; Palmer and Rosenquist, 1974; Gilbert, 1977; Hammond and Ahmed, 1985; Hammond and MacKay, 1977; LeVay and Voigt, 1988), their intracortical and extracortical connections (Singer *et al.*, 1975; Gilbert and Kelly, 1975; Martin and Whitteridge, 1984; Gilbert and Wiesel, 1983) and increasing evidence suggests that they participate in selective interactions (Malpeli, 1983; Malpeli *et al.*, 1986; Schwark *et al.*, 1986; Weyand *et al.*, 1986; Bolz and Gilbert, 1986; Schwarz and Bolz, 1989).

Response variability

In addition to the heterogeneity in temporal firing patterns among cell types we have extended and confirmed the previous finding that the oscillatory response is not phase-locked to the visual stimulus (Gray and Singer, 1987a,b, 1989; Eckhorn *et al.*, 1988). This result holds for stationary as well as moving stimuli. Examination of the spike trains and computation of the auto-correlograms for each trial revealed that the latency for onset, phase, frequency and duration of the oscillations varied from trial to trial. This result was supported by the occurrence of flat distributions in the shift-predictor (Perkel *et al.*, 1967) of the auto-correlograms (Gray and Singer, 1989). We conclude from these results that the rhythmic firing is not related to the fine spatial structure of the neuron's receptive field. Were this to be the case a yet undiscovered property of cortical receptive fields would have to be postulated to account for the data. In order to generate a 50 Hz rhythm a mechanism would be required in which a stimulus moving at 2°/s would pass through subunits of the receptive field having a spatial frequency of approximately 25 cycles per degree. No evidence that we are aware of points to cortical receptive fields having such a large and finely spaced number of excitatory or inhibitory subunits (Hubel and Wiesel, 1962; Movshon *et al.*, 1978a,b,c). Additionally, in order for such a mechanism to account for the synchronization of oscillatory responses among nearby cells (Gray and Singer, 1989; Gray *et al.*, 1989) a precise alignment of receptive fields would have to be postulated. Such an arrangement is inconsistent with the wealth of evidence demonstrating receptive field scatter (Hubel and Wiesel, 1962; Gilbert, 1977).

Feature dependence of oscillatory responses

The third general category of results presented here demonstrate that the temporal properties of the oscillatory responses depend on the feature properties of the stimulus. In many instances we have observed large amplitude responses with little or no oscillatory behaviour, only to find that after a change in the stimulus a clear oscillatory response can be evoked. This finding suggests that the particular pattern of functional interaction a given cell may participate in will depend on the properties of the stimulus used (Gray *et al.*, 1989; Engel *et al.*, 1990). With respect to this result oscillatory neuronal responses occur most often, and with greatest magnitude, when: (i) an optimally orientated visual stimulus is delivered through both eyes simultaneously or to the dominant eye; (ii) the velocity of the stimulus movement is in the range of 1−12°/s; and (iii) when the length of a light bar stimulus is equal to or extends beyond the dimensions of the excitatory receptive field. The combined presentation of optimally and orthogonally orientated light bars often reduced or disrupted the oscillatory responses. Stimulus velocity was the only feature parameter tested in which we observed a direct relationship between a stimulus parameter and the oscillation frequency.

These findings suggest that network interactions within the cortex play a crucial role in shaping the temporal properties of the oscillation. Moreover, they raise the possibility that: (i) oscillatory interactions occur preferentially during binocular fixation; (ii) objects moving at different velocities in the visual field may be segregated within the cortex by oscillatory responses having different frequencies (i.e. fast moving objects at high frequencies and more slowly moving objects at lower frequencies); (iii) changes in the synchronization between separate cell groups responding to long co-linear contours may involve the recruitment of additional synchronously active populations of cells (Gray *et al.*, 1989); and (iv) multiple overlapping stimulus features present within the receptive field can modify the temporal pattern of oscillatory responses. In addition, responses to stimuli orientated as much as ±67 degrees from the optimum occasionally still exhibit a rhythmicity at a frequency close to that of the optimal orientation. This supports our previous findings that oscillatory interactions can occur between orthogonally orientated cells even when they are driven by a single stimulus which is nonoptimal for either or both of the cells (Gray *et al.*, 1989; Engel *et al.*, 1990). These feature dependent properties of the oscillatory responses suggest that the interactions among spatially distributed populations of cells will depend critically on the stimulus conditions.

Mechanisms of oscillatory response generation

Two essential characteristics distinguish oscillatory from nonoscillatory cells: first, the former often fire bursts of action potentials at instantaneous rates as high as 200−400 Hz and second, the bursts appears at regular intervals of 16−30 ms. This behaviour gives rise to the composite pattern which we term an oscillation. The similarity between this rhythmical pattern of burst firing and the regenerative burst responses of neurons in layers 4 and 5 recorded *in vitro* (Connors *et al.*, 1982; McCormick *et al.*, 1985) suggest a possible correspondence between these cell types. Moreover, recent evidence that intrinsically bursting neurons can generate sustained periods of rhythmic activity is consistent with this notion (Agmon and Connors, 1989; Silva *et al.*, 1989). The laminar distribution of oscillatory cells in our sample is more widespread than the restricted localization of bursting cells in layers 4 and 5. However, in a recent report bursting cells have been identified in layers 2−4, suggesting the possibility of a sparse distribution of these cells in upper cortical layers (Jassik-Gerschenfeld *et al.*, 1989). In any case the determination of a correspondence between intrinsically bursting neurons and oscillatory cells will require a direct demonstration.

Nevertheless, a number of experimental, as well as theoretical, studies have demonstrated that rhythmic patterned firing is controlled in part by a combination of intrinsic membrane conductances (Llinas, 1988). These intrinsic membrane properties influence and control burst firing (Johnston *et al.*, 1980; Stafstrom *et al.*, 1985; Schwindt *et al.*, 1988; Berman *et al.*, 1989) as well as the generation of sustained rhythmical responses in the range of 5−15 Hz (Llinas, 1988; Alonso and Llinas, 1989; Silva *et al.*, 1989). There is to our knowledge, with the exception of one recent report (Llinas and Grace, 1989), no compelling evidence that intrinsic membrane properties alone give rise to repetitive bursts of action potentials at intervals of 20 ms during sustained depolarizations. Were this to be the case, however, it remains to be explained how such a mechanism could account for the broad dynamic range of oscillation frequencies and amplitudes observed here. Thus, it is likely that the cortical circuitry, in which these burst firing

neurons are embedded, makes a substantial contribution to the control of the inter-burst interval and thereby the frequency of oscillation (Chagnac-Amitai and Connors, 1989).

The nature of the intracortical interactions underlying the control of oscillation frequency and amplitude are unknown. However, experimental and theoretical evidence from the olfactory system suggest that the magnitude of both excitatory and inhibitory interactions are likely to exert a powerful influence in shaping the response amplitude and oscillation frequency (Freeman, 1975, 1979, 1985; Gray and Skinner, 1988). In the mammalian olfactory bulb, a structure known for its powerful 40–80 Hz oscillations, the generation of high frequency oscillatory activity is thought to depend on feed-back inhibition from GABAergic interneurons (Freeman, 1975). The oscillatory responses of the inhibitory interneurons, the granule cells, show a 1/4 cycle phase lag with respect to the excitatory output neurons of the bulb, the mitral cells. This result conforms to the expectation of a simple negative feedback model. Changes in the frequency of oscillation, observed experimentally in alert animals (Freeman, 1975; Gray and Skinner, 1988), have been effectively modelled by specific changes in the strength of excitatory synapses onto excitatory cells as well as the strength of the feedback inhibition (Freeman, 1979). Thus, it is likely that a number of complex circuit interactions involving at least feed-back inhibition and mutual excitation will participate to determine the oscillation amplitude and frequency. Our finding that the pattern of the oscillatory response depends to a substantial extent on stimulus configurations supports the conjecture that, similar to the olfactory system, dynamic properties of the intracortical network may be important for the generation of oscillatory responses in the visual cortex.

Abbreviations

ACF auto-correlation function
LFP local field potential
PSTH post-stimulus-time histogram

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