Phase Relationships Between Adjacent Simple Cells in the Visual Cortex

Abstract. *Adjacent simple cells recorded and "isolated" simultaneously from the same microelectrode placement were usually tuned to the same orientation and spatial frequency. The reponses of the members of these "spatial frequency pairs" to drifting sine-wave gratings were cross-correlated. Within the middle range of the spatial frequency selectivity curves, the responses of the paired cells differed in phase by approximately 90°. This phase relationship suggests that adjacent simple cells tuned to the same spatial frequency and orientation represent paired sine and cosine filters in terms of their processing of afferent spatial inputs and truncated sine and cosine filters in terms of the output of simple cells.*

We have recorded from "pairs" of adjacent simple cells in the visual cortex of the cat. Recording situations in which two distinct action potentials of decidedly different amplitude can be recorded simultaneously from a single microelectrode occur infrequently. However, these paired responses provide a unique opportunity to determine how adjacent visual neurons differ in the encoding of such important characteristics as orientation preference (*1*), spatial frequency preference (*2*), and relative phase between pair members.

Initially we examined the records from 16 cell pairs. These were obtained in the course of 24 recent experiments for which the original purpose was to compare the response of simple and complex cells to drifting sine-wave and square-wave gratings (*3*) and from a review of the data tapes from other work on simple cells from this laboratory (*4*). In four cases, one cell was simple and the other complex; these pairs were not analyzed further. In the remaining 12 cases both pair members were simple cells. Within each of these pairs, both cells were tuned to the same orientation and direction within 5° to 10° and to the same spatial frequency within one-fourth octave. In these cases, a cross-correlation of each cell's response to drifting sine-wave gratings afforded an opportunity to determine the extent of spatial overlap of the adjacent receptive fields as measured by their difference in spatial "phase." Information of this type has not previously been reported for neurons in the visual cortex nor, to our knowledge, for a pair of adjacent neurons anywhere along the visual pathways.

General methods of anesthesia, recording, presentation of visual stimuli, and evaluation of preferred spatial frequency have been presented in detail elsewhere (*4*). The criteria of Hubel and Wiesel (*1*) have been used for the identification of simple cells. Cross-correlation techniques were used to define the

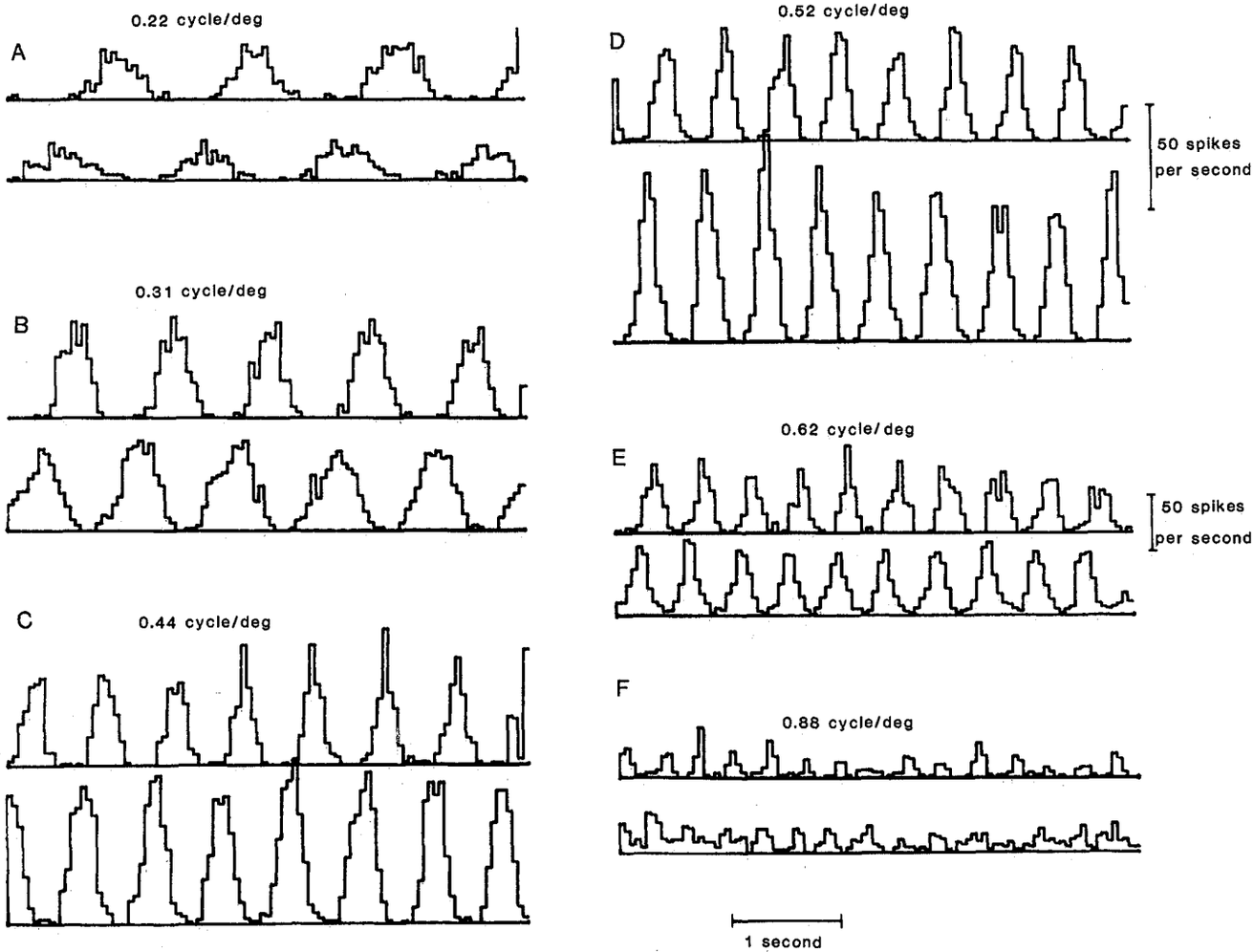

Fig. 1. Responses of two adjacent simple cells to six different spatial frequencies recorded simultaneously from the same microelectrode placement. The upper tracings in each section represent the responses of one cell, and the lower set represents the responses of the other. The calibration in (D) applies to (A) to (C) and (F) as well.

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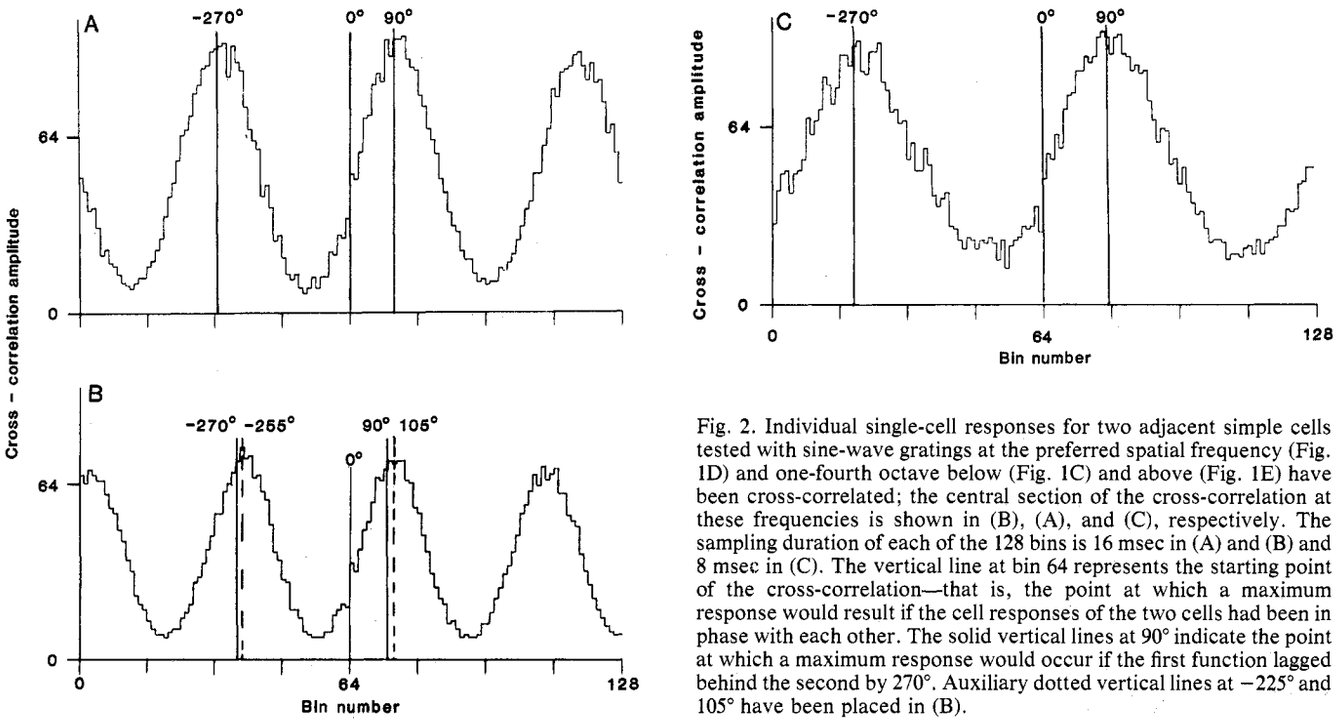

Fig. 2. Individual single-cell responses for two adjacent simple cells tested with sine-wave gratings at the preferred spatial frequency (Fig. 1D) and one-fourth octave below (Fig. 1C) and above (Fig. 1E) have been cross-correlated; the central section of the cross-correlation at these frequencies is shown in (B), (A), and (C), respectively. The sampling duration of each of the 128 bins is 16 msec in (A) and (B) and 8 msec in (C). The vertical line at bin 64 represents the starting point of the cross-correlation—that is, the point at which a maximum response would result if the cell responses of the two cells had been in phase with each other. The solid vertical lines at 90° indicate the point at which a maximum response would occur if the first function lagged behind the second by 270°. Auxiliary dotted vertical lines at −225° and 105° have been placed in (B).

phase differences in the responses of pairs of simple cells recorded simultaneously from a common microelectrode placement in response to drifting sine-wave gratings (*5*). Most cross-correlations were carried out on a PDP-12 computer according to the STAP-12 program of Wyss and Handwerker (*6*).

Table 1. Preferred spatial frequency, preferred orientation, and interpair phase shift measured at the preferred spatial frequency and preferred orientation are given for 12 pairs of simple cells. All receptive fields were within 5° of the area centralis and could be (i) even-symmetric and with either on or off centers or (ii) odd-symmetric. The cells have been ordered by increasing preferred spatial frequency. The optimum orientation was measured counterclockwise from the horizontal axis. In the two pairs where the interpair phase shift varied within one-fourth octave of the preferred spatial frequency, the lower value of the interpair phase shift was used in the estimation of the mean.

Simple cell pair	Spatial frequency (cycle/deg)	Preferred orientation (degrees)	Interpair phase shift
1	0.3	90	90° to 95°
2	0.3	0	82°
3	0.32	0	90°
4	0.36	0	104°
5	0.39	20	92°
6	0.61	45	90°
7	0.62	50	105°
8	0.65	45	90°
9	0.75	90	90° to 105°
10	0.82	45	87°
11	1.0	165	95°
12	1.5	120	90°

The average response histograms to optimally oriented drifting sine-wave gratings for a cell pair tuned to a common spatial frequency are shown at six different spatial frequencies in Fig. 1. The responses consist of sine waves in which the negative components may be truncated either partially or completely (*4*, *7*) at the level of zero cell firing. At spatial frequencies close to the preferred frequency, a phase difference of about one-fourth cycle, or 90°, may be noted (Fig. 1, B to E).

The cross-correlations of the original data from the cell for which average response histograms are displayed in Fig. 1, C to E, are shown in Fig. 2. The lead of the response of one cell over the other member of the pair was approximately 90°, and similarly, the lag of the first cell with respect to the previous cycle of the second cell was approximately 270°. The phase shift at the preferred spatial frequency (Fig. 2B) was close to 105°, whereas a 90° shift appeared at spatial frequencies one-fourth of an octave lower (Fig. 2A) or higher (Fig. 2C).

We have also plotted the relative phase shift for four pairs of adjacent simple cells with common preferred spatial frequencies as a function of the spatial frequency of the test grating (Fig. 3). In three cases (B to D) the phase shift was well within 5° of 90°. In the fourth case (A), the phase shift at the preferred spatial frequency (F_0) was 105°, but dropped to 90° at one-fourth octave on either side of F_0. The slightly greater phase shift at F_0 here might result from the exceptionally strong response of the lead cell (lower pair member in Fig. 1D), thereby bringing it to firing level relatively sooner than with weaker stimuli. In any case, the phase shift between pair members in the central half-octave range of the spatial frequency selectivity curve closely approximates 90°. Results for all 12 pairs are summarized in Table 1. The

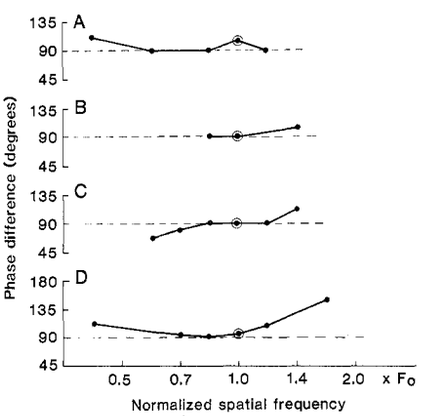

Fig. 3. Relative phase differences between the responses of adjacent simple cells as a function of spatial frequency. For each pair, the preferred spatial frequency has been normalized to a value of 1.0, so that the relative phase shift at the preferred spatial frequency (open circles) and at comparable intervals on either side of this frequency can be compared. The horizontal dashed lines indicate a phase shift of 90°.

mean value of the interpair phase shift was 92.1° ± 6.5°.

In some cases (Fig. 3, A and C), the phase shift across an extended range of the spatial frequency spectrum remained close to 90°. This finding indicates that the axes of the receptive field centers must be the same and thus rules out the possibility that the two receptive field profiles are identical but simply shifted with respect to one another. In fact, if cells have the same spatial tuning curve (Fig. 1) and a 90° phase shift independent of frequency (Fig. 3A), their receptive fields must be conjugate pairs—that is, one field with even symmetry and one with odd symmetry around the same axis.

Moreover, in the last two pairs studied, we used stationary flashed stimuli to categorize the receptive field type of each pair member separately with the aid of the spike amplitude discriminator and audio amplifier. In both cases, one pair member had an approximately even-symmetric receptive field and the other an odd-symmetric profile. Marčelja (*8*) has shown that the even-symmetric and odd-symmetric receptive field profiles of simple cells can be fitted to the product of a Gaussian and either a cosine or sine function, respectively. Marčelja realized that these functions represent the elementary signals described by Gabor (*9*). When paired, these functions permit simultaneous maximal localization of a signal in space and spatial frequency. Simple cells, like Gabor functions, can be considered to represent spatial frequency filters of medium bandwidth (full band width ~ 1 octave) that are reasonably well localized in space.

How might the sequence of simple cells with incremental 90° phase shifts and common spatial frequency and orientation preference be arrayed within the striate cortex? Hubel and Wiesel (*10*) have shown that "columns" subserving constant preferred orientations are actually parallel sheets or slabs running perpendicular to the cortical surface. Kronauer (*11*) has suggested that the 90° phase increments may define the orthogonal processing function along each sheet. The simple cell pairs may constitute subsets of a much longer contiguous cortical sequence. For example, progressive shifts of phase of 90° would imply a uniform stepwise translation of receptive fields over the retina that could be extended in a long sequence across the cortex.

The finding that the negative components of the response of a simple cell to a drifting sine-wave grating are so often markedly or completely truncated (*4, 7*) requires consideration. In principle, the "information" lost by truncation could be preserved if there exists, perhaps elsewhere in the orientation column, another pair of simple cells similarly tuned to orientation, direction, and spatial frequency, but with receptive fields of reversed polarity to those of the observed pair. The members of the second pair would selectively respond when the responses of the first pair were truncated. Between these four cells, the available information would specify sine and cosine components and thereby suffice to specify the amplitude and phase information at one spatial frequency, orientation, and direction over the receptive field region. A single pair would have sufficed (*12*) had it not been for the truncation problem.

When Pollen *et al.* (*13*) first proposed that striate neurons carry out a two-dimensional spatial frequency analysis over "a restricted region of visual space," they assumed that this analysis began at the complex cell stage. Recent research has established that both simple and complex cells participate in this analysis (*3, 14*).

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5. Because each sine-wave grating drifted across the receptive field at a constant velocity, the phase difference between the responses of the two cells could be measured either in spatial or temporal units. At least two different bin widths from 2 to 16 msec were used at each tested spatial frequency so that a maximum resolution of the data consistent with a high density within each bin could be obtained. There were 128 bins available for displaying the central section of the cross-correlation. Bin 64 represented the start of a cross-correlation. We specified the precise position of the maximum response from the start of the cross-correlation by determining the extent along the *x* axis occupied by each full cycle of the cross-correlation and assigning a 360° phase shift for this interval. We could then specify the position in degrees of each maximum from the start. The accuracy of this estimate depended on the bin width and the smoothness of the curve, which in turn allowed us to determine the maximum. We believe that, with care, this determination could be made to within 5°.
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All-Female Fish: A Cryptic Species of *Menidia* (Atherinidae)

Abstract. *Electrophoretic evidence revealed the common occurrence of an all-female species of* Menidia *(Pisces: Atherinidae) at two localities separated by 280 kilometers on the Gulf Coast of Texas. This finding adds significantly to the known taxonomic spectrum of unisexuality in fishes and demonstrates that unisexuality may be more common among fishes that do not bear live young than is generally suspected.*

Electrophoresis of proteins in 18 widely scattered Texas populations of the genus *Menidia* (Pisces: Atherinidae) revealed an undescribed species consisting entirely of females. The new form is found with two bisexual species, *Menidia beryllina* and *M. peninsulae*, in brackish waters at two widely separated areas on the Texas Gulf Coast. Because of high morphological similarity to the two bisexual species (Fig. 1), which are themselves difficult to separate (*1, 2*), the unisexual form has gone undetected despite its abundant occurrence in Nine Mile Point Pond, a site of intensive ichthyological activity (*3*), including one study (*4*) on *Menidia* taxonomy.

Most of the few well-studied unisexual animal species apparently arose ancestrally as hybrids between closely related bisexual species (*5–7*). Thus unisexual forms represent a potentially major source of undetected species, especially when, as in the present example, the apparent parental forms are highly similar. Since discovery (*8*) of the Amazon mollie, *Poecilia formosa*, the first known unisexual vertebrate, only about 40 natu-

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