Synchronous Activity in Cat Visual Cortex Encodes Collinear and Cocircular Contours

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Samonds, Jason M., Zhiyi Zhou, Melanie R. Bernard, and A. B. Bonds. Synchronous activity in cat visual cortex encodes collinear and cocircular contours. J Neurophysiol 95: 2602–2616, 2006. First published January 4, 2006; doi:10.1152/jn.01070.2005. We explored how contour information in primary visual cortex might be embedded in the simultaneous activity of multiple cells recorded with a 100-electrode array. Synchronous activity in cat visual cortex was more selective and predictable in discriminating between drifting gratings and concentric ring stimuli than changes in firing rate. Synchrony was found even between cells with wholly different orientation preferences when their receptive fields were circularly aligned, and membership in synchronous groups was orientation and curvature dependent. The existence of synchrony between cocircular cells reinforces its role as a general mechanism for contour integration and shape detection as predicted by association field concepts. Our data suggest that cortical synchrony results from common and synchronous input from earlier visual areas and that it could serve to shape extrastriate response selectivity.

INTRODUCTION

The primary visual cortex has traditionally been viewed as a network of filters or feature detectors, each sampling localized regions of the visual field (Hubel and Weisel 1962). There remains considerable debate on how features are integrated for object recognition and segmentation. This question becomes especially critical when considering that the firing rate of each cell varies across multiple features (e.g., orientation, spatial frequency, temporal frequency, contrast, context) resulting in ambiguity. One proposed solution is that feature detectors are integrated through synchronous activity (Singer and Gray 1995). Synchronous integration is an intriguing solution because it could also provide an elegant resolution to the binding problem (von der Malsburg 1999; but see also Shadlen and Movshon 1999).

The first experimental evidence for the involvement of synchronous activity in feature integration used coherent collinear stimulation such as drifting light bars (Eckhorn et al. 1988; Gray et al. 1989; Ts’o et al. 1986). The observed synchrony required that pairs of cells had similar orientation preferences and collinear receptive fields (RFs). Collinearity is actually just one special case of the more general property of cocircularity (Parent and Zucker 1989). Cocircular RFs are defined as having orientation preferences with the same angle, but opposite sign, with respect to a line connecting the center of the two RFs—i.e., tangent to the same circle (Parent and Zucker 1989) (Fig. 1). Cocircularity is a ubiquitous structure in natural scenes (Elder and Goldberg 2002; Geisler et al. 2001; Sigman et al. 2001; see also Chow et al. 2002) and has been proposed as the foundation of contour integration (Field et al. 1993). The framework is known as the association field, where the chances of contour segments being part of one continuous contour increase with proximity and similarity in their orientation. Each segment of an integrated contour falls on the same circle as another segment. The idea is that in nature, contours are predominantly linear with a decreasing probability of greater curvature (aligning on progressively smaller circles).

The goal of our current study was to see if synchronous activity predictably exists for cell pairs that differed in orientation preference, but the RFs of which still followed cocircularity and association field rules. Extending the collinear synchronous results to cocircular RFs in general is necessary if synchrony is to be considered to play some role in integrating complex contours and shapes. We recorded from large groups of cells simultaneously in areas 17 and 18 of anesthetized cats and found that particular subgroups of cells dynamically synchronize depending on the incoming visual information (based on cocircularity). Synchronous activity matched the association field rules and stimulus curvature much more reliably than the average firing rate because synchrony depended primarily on local contour information and was not prone to response ambiguities outside of the local RFs. We conjecture that the integration of global contour information begins with synchronous activity within cell groups in early visual areas such as V1. Extrastriate cortex could then respond to complex shapes and curvature by detecting this synchronous activity.

METHODS

Physiological preparation and recording

Experimental procedures were performed under the guidelines of the American Physiological Society and Vanderbilt University’s Animal Care and Use Committee and are described in detail elsewhere (Samonds and Bonds 2005; Samonds et al. 2003, 2004). Two cats were anesthetized with propofol and N2O and paralyzed with pancuronium bromide. A Bionics (now Cyberkinetics) 10 × 10 multi-electrode array (400-μm spacing) was pneumatically inserted to a fixed depth of 0.6 mm (Fig. 2). Seventy and 98 channels recorded single- or multiunit activity for each cat, respectively. However, we could not isolate spiking activity with thresholding for all channels due to low signal to noise.

Details about the reliability of single-unit recordings with this array and spike sorting procedures can be found in Samonds and Bonds...
passing through the center of each receptive field (RF) at the preferred orientation must be tangent to the same circle. (2005). Here we did not include multiple units that were recorded and resolved from a single channel (i.e., all single units reported in this article are from different electrodes). Spike sorting was used to isolate the most robust single unit (e.g., see Fig. 2B, right) and remove noise and artifact on each channel (Shoham et al. 2003). We isolated 28 and 23 single units from different orientation-selective activity driven by drifting sinusoid gratings (Fig. 2, A and B, respectively). The response to the preferred orientation had to be at least two times that from the worst orientation (orientation tuning was typically robust and narrow: e.g., see Fig. 7). The 51 cells provided 631 pairs of cells, for cross-correlation analysis.

Due to tissue damage caused by removing the array, we were unable to perform histological analysis on the recording sites after recording. However, based on the relationship between electrode positions and Horsley-Clark coordinates and response characteristics, we believe that >92% (47/51 cells) of our sample was in area 17 while the remaining 8% (4 cells) was in area 18 (see Fig. 2). Based on our estimation, the area 18 cells contributed 9 pairs (5%) to our sample of synchronous pairs (n = 188 pairs) with all pairs composed of one area 17 and one area 18 cell. The fixed insertion depth virtually ensures recordings were in superficial layers. The curvature of the brain leads to some variation of electrode depth with a maximum depth of 0.6 mm. This depth combined with the possibility of recording activity a few hundred micrometers below the electrode leaves only a very small probability of our sample including layer 4 cells. Forty-nine out of the 51 cells were complex (Hubel and Weisel 1962; Skottun et al. 1991) with a mean F1/F0 = 0.34 ± 0.03 (n = 51 cells).

Quantifying synchrony

We quantified synchrony using the "effective connectivity" cross-correlation histogram (CCH) derived from the joint poststimulus time histogram (JPSTH) (Aertsen et al. 1989; see also Samonds and Bonds 2005; Samonds et al. 2003; Sillito et al. 1994; Snider et al. 1998). The cross-product of the PSTHs (expected correlation) is subtracted from the JPSTH (observed correlation) and then normalized by the SD of the PSTH predictor (normalized JPSTH; Eq. 9 in Aertsen et al. 1989). We then create a CCH by integrating along the principal diagonal of this two-dimensional matrix (Aertsen et al. 1989). Aertsen et al. (1989) refer to this CCH as the normalized cross-correlogram or effective connectivity. We represent the magnitude as the percentage of the maximum possible effective connectivity (all spikes correlated; correlation coefficient ranging from −100 to 100%). We quantify what we will refer to throughout the article as synchrony by measuring the 1-ms peak at or near zero in the CCH. We considered synchrony significant when the peak was at least two times the random fluctuations or noise in the CCH (0.1–0.3%).

Although the cross-product of the PSTHs is conceptually the same as the shift predictor, the methods are distinct from each other and the cross-product provides a much smoother predictor function (Aertsen et al. 1989). The normalization strategy of the JPSTH was also chosen to contribute as little noise as possible to the cross-correlation estimate (Aertsen et al. 1989). Based on models with known correlation strengths and temporal profiles, Aertsen et al. (1989) found the SD of the PSTH-based predictor (described in the preceding text) as the best choice for true normalization (due to its relatively small dynamic range) (see also Ito and Tsuji 2000; Palm et al. 1988). In addition, the SD of the predictor is equal to the square root of the product (geometric mean) of the autocovariation histograms and the resulting normalized value is equivalent to Pearson’s correlation. We find that with this normalization procedure, there is only a weak relationship between synchrony and firing rate (r² = 0.13 for sum of rates and r² = 0.16 for product of rates) (see also Fig. 13 in Samonds and Bonds 2005).

The second concern with any cross-correlation method is that fast correlations (tens of milliseconds) may not necessarily represent true connectivity-based (anatomic) correlation. Brody (1998, 1999a,b) has shown that long-term (tens of seconds) or trial-by-trial covariation of firing rates, covariation of response latency, and covariation of excitability can produce what might be easily interpreted as correlated activity resulting from anatomical connections (short-term correlations) (however, see also Kirkland et al. 2000). We explicitly chose the relatively vague and benign term synchrony for this very reason. Correlation and connectivity both implicitly suggest knowledge of the underlying causes for the observed firing rate statistics. What is debatable is that the Aertsen et al. (1989) measurement describes the deviation of the activity from independence (Brody 1998, 1999a,b; Ito and Tsuji 2000). Although deciphering the origins of this deviation is important, we are at present primarily interested in describing the stimulus dependence and dynamic behavior of the synchrony. For more recent progress on these topics, see Gerstein and Kirkland (2001) and Kass et al. (2005). We see very little covariation or correlation among the trial-by-trial firing rates (r² < 0.1 and always < 0.3), and there are not clear relationships between PSTHs and CCHs. There is some weak broad correlation (beyond ±100 ms) observed that is likely caused by common inhibitory input (Moore et al. 1970; Ts’o et al. 1986).
Visual stimulation

We tested responses to coherent cocircular stimulation using drifting sinusoidal concentric rings (Fig. 3A). The rings drifted outward and were presented within a 16° circular aperture on a mean luminance background. The center locations were strategically chosen based on RF loci of the population to test conditions that would bias predicted synchrony between cells with clear orientation preference differences (>30°) (see Fig. 3, C and D). However, each experiment included hundreds of pairs of cells, most requiring a unique ring origin, so 9–16 locations were chosen to test as many pairs as possible in an individual experiment. Our approach was highly probabilistic. Even though there were large numbers of cell pairs, it was not axiomatic that every cell pair would demonstrate constructive interactions, so stimuli had to be optimized for the population to maximize our yield of data that could be analyzed in detail. Pair-by-pair testing for 631 pairs of cells is not possible with our preparation in just two recording sessions. We chose concentric rings because this stimulus is very efficient because it minimizes trials by testing for varying curvature and cocircular relationships at multiple locations simultaneously. This strategy allowed us to synchronize 51 pairs of cells with differences in orientation preference ranging from 10 to 80° during the two experiments with rings stimulation.

We used drifting sinusoidal gratings to test responses to coherent collinear stimulation (Fig. 3B). The orientation and direction were varied in 10° increments over all possible orientations and directions, whereas all other grating parameters were fixed (spatial frequency = 0.5 c/°, temporal frequency = 2.0 Hz, contrast = 50%). All properties except orientation were the same for cocircular and collinear stimulation.

Linear and circular gratings on a mean luminance background provided the strongest responses, enhancing reliable estimation of response properties. Based on psychophysical considerations, we predicted that the rings and gratings offered the greatest chance of revealing the underlying mechanisms of contour integration because their contours are parallel (Alais and Lorenceau 2002; Geisler et al. 2001; Polat and Negri 1998; Polat and Tyler 1999; however, see Solomon and Morgan 2000), circular (Alais and Lorenceau 2002; Field et al. 1993; Geisler et al. 2001; Pettet 1999; Pettet et al. 1998; Pizlo et al. 1997), and are enclosed (Kovács and Julesz 1993; Pettet et al. 1998). We were interested in clearly revealing the dynamics of response properties from collinear to curvilinear stimulation. We did not explore segmented contours or contours embedded within noisy elements because we wanted to maximize our chances of contour integration among a variety of cells. We believe it is important to extend our results to some of the psychophysics tests such as segmented contours, but because the segmented contours are still detected and grouped together, they do not really provide a definitive test for contour integration [the psychophysics results suggest the response properties or synchrony would simply deteriorate (Alais and Lorenceau 2002; Beaudot and Mullen 2003; Pizlo et al. 1997); see also corresponding neurophysiologic data (Gray et al. 1989; Kapadia et al. 1995)].

Selection criteria

A total of 127 of a possible 631 pairs of cells were chosen for cocircularity analysis based on responsiveness and the spatial relationship between the RFs and the stimulus (Fig. 4). In addition to requiring that each cell had orientation tuning (described in the preceding text), we required that the pair of cells responded with a total average firing rate of ≥5 spikes per second (sp/s) for either gratings or rings and had significant synchrony (see preceding text) for one of the two stimulus conditions. Our detailed analysis (Figs. 8, 9, and 12) on only a limited portion of our entire dataset was important to ensure that we made direct comparisons between the two stimulus conditions and direct reliable comparisons between the two measured response properties. At least with respect to firing rates, this smaller sample was not significantly different from the entire sample ($P > 0.38$).

We used bars of light rear-projected onto a large tangent screen to estimate RF sizes (mean = 3.9 ± 0.2°) and locations (Fig. 3, C and D). Receptive fields of cells in a pair had to have minimal overlap so that stimulus-response predictions were unambiguous. The mean RF overlap for each cell for pairs of cells with unambiguous RF relationships was 35.0 ± 1.8%. Firing rate and synchrony measurements were made for the rings and gratings that provided the best match with the preferred orientation of both cells. To make predictions about which stimulus would lead to a greater response, it had to be clear whether the segment of the rings or the gratings passing through the two respective RFs was closer to the preferred orientation for both cells. Therefore the quantitative criterion for the classes was that the corresponding rings or gratings contour had to match the RF orientations better than the complementary stimulus by ≥10° (because we used 10° increments). For example, rings would drive a pair of cells with a >40° difference in orientation preference better than gratings only if the ring segments are within ±20° of the preferred orientation for both cells. This criterion for both cells is impossible with larger amounts of receptive overlap—hence the ambiguity. Additionally, pairs of cells that were not aligned with the rings (because a limited number of locations were tested) were also not included because we could not make a direct comparison with the gratings condition.

Cocircularity analysis

For each pair of cells, we calculated the ratio ($RPI$, rings preference index) for both the total average firing rate and synchrony for rings ($R$) versus gratings ($G$; the optimal rings and gratings)

$$RPI = \frac{R - G}{R + G}$$

We specify this ratio as $RPI$, when it is calculated on the basis of firing...
rate and RPI, when it is calculated on the basis of synchrony. We used a standard sigmoid model fit for RPI versus the orientation preference difference between the cell pair (which we term cocircularity) \( x \) to see how well the synchrony or total average firing rate varied with cocircularity on a pair-by-pair basis

\[
RPI(x) = \frac{A}{1 + e^{B(x-x_0)}}
\]

(2)

We used a standard Gaussian model fit for our synchrony and firing rate measurements for grating stimulation, where \( x \) is cocircularity and \( f(x) \) is the total average firing rate or synchrony

\[
f(x) = Ae^{-(x-x_0)^2}
\]

(3)

The Gaussian fit was chosen because the total average firing rate and synchrony should decline with collinear gratings with increasing or decreasing cocircularity (i.e., both are absolute increases in the orientation preference difference). We used the sigmoid fit (Eq. 2) for synchrony and firing rate measurements for rings stimulation because the total average firing rate and synchrony should decline only for decreasing cocircularity. The models were otherwise arbitrarily chosen simply to show how much the variance of the total average firing rate and synchrony was related to stimulus-RF relationships (i.e., cocircularity) with regression analysis. The difference between \( R^2 \) measurements for total average firing rate and synchrony are more important than the absolute \( R^2 \) values, which are likely to be degraded by both response properties being dependent on additional spatiotemporal stimulus properties beyond contour/orientation information (e.g., spatial frequency, temporal frequency), which were not optimized for each pair of cells. Confidence intervals were calculated by bootstrapping pairs (Efron and Tibshirani 1993).

**RESULTS**

To provide an adequate sample of cells with a variety of cocircular RF relationships, we recorded simultaneously, with 100-electrode arrays, from 28 and 23 cells in striate cortex of two cats, providing a total of 51 cells and 631 pairs of cells (see Fig. 2). We tested responses to coherent cocircular stimulation using drifting sinusoid concentric rings (Fig. 3A) and tested responses to coherent collinear stimulation using drifting sinusoid gratings (Fig. 3B). Nine to 16 locations in the visual field were strategically chosen for the ring centers to match the ring contours to the preferred orientations of pairs of cells with obvious differences in preferred orientation (see Fig., 3, C and D). For gratings, orientations were varied in 10° increments over a range of 360°. All other stimulus properties were the same for both rings and gratings. Our stimulation paradigm produces data with a distribution that tends to be bimodal rather than continuous with respect to stimulus feature space. This allows us to show significant differences among the distributions. We chose this strategy because the physiological data would not be reliable enough to make significant parametric comparisons to psychophysical (access to all cells) and natural scene (very large databases) statistical distributions with respect to association field concepts.

Synchrony was quantified as the peak height of the rate-normalized cross-correlogram (Aertsen et al. 1989) with the quantity expressed as the percentage of the maximum possible synchrony (i.e., percent correlation; ranging from -100 to 100%). Peak widths were consistent (~10 ms width) so area under the peak provides qualitatively similar results. All of our pairs were recorded in the same layer (600 \( \mu \)m, putatively II–III) and thus would have some chance of integration at the next stage of visual processing. An evaluation of the utility of synchrony in propagating information requires that it be compared against some other mechanism. Here we compare it against the firing rate, which is the usual metric for neural signaling. There are however two different ways of quantifying the firing rate of cell pairs, depending on the time constants of the recipient cell layer. If the time constant is reasonably long, then the firing rate is simply integrated without regard to temporal structure, and its effectiveness can be modeled by adding the average firing rate of the two cells. If the time constant is short, then only coincident spikes are effective. The probability of coincident spikes is simply equal to the product of the probabilities of each cell firing within the time constant interval, so the receiving layer acts as an effective multiplier of firing rates. Both mechanisms may be represented at different times, in that time constants are dynamic and dependent on the activity of the cell (e.g., Azouz and Gray 2003). In this paper, we chose to analyze firing rate on the basis of the sum because it provides a test of the relative effectiveness of two different
processing strategies. We have also performed similar analyses using the product metric (see Supplemental Materials)1 and show that the results remain qualitatively unchanged with regard to the relationships between contour information and firing rates. Our synchrony measurements are only weakly related to both the sum and product of the firing rates (see METHODS) and provide an additional critical dimension to encode visual information.

We first examine our data with a broad perspective to see how firing rate and synchrony match the predictions made by the association field theory. We then take a closer look at the data by characterizing the RF properties. We use these properties to make predictions on how pairs of cells will respond to gratings and rings stimulation (i.e., varying degrees of curvature). Then, we test these predictions first very generally based on population statistics and rings and gratings stimuli. Next we systematically test these predictions on a pair-by-pair basis with respect to the degree of curvature. Finally, we examine cross-correlation properties to gain insight into the possible underlying mechanisms of synchronous integration of contour information.

Visual cortical pairs and association field predictions

Collinear contours exceed cocircular contours in natural scenes (Geisler et al. 2001; Sigman et al. 2001), and collinear contours are more easily detected psychophysically than curvilinear contours (Beaudot and Mullen 2001; Field et al. 1993; Geisler et al. 2001; Pettet 1999; Pettet et al. 1998; Pizlo et al. 1997; Polat and Sagi 1994). This is consistent with one of the primary rules of the association field theory—segments are less likely to be part of the same contour with greater differences in their orientations (i.e., greater curvature) (Elder and Goldberg 2002; Field et al. 1993; Geisler et al. 2001; Polat and Sagi 1994; Sigman et al. 2001). A second rule is that segments are less likely to be integrated with increasing distance between them. Cortical organization should reflect these principles in two ways: orientation-tuned cells are connected when their RFs have cocircular alignment and the number of connections decreases with increasing RF distance and increasing difference in orientation preference. Anatomical evidence tends to support these concepts (Bosking et al. 1997; Lund et al. 2003; Malach et al. 1993). Overall we would therefore predict enhanced activity (firing rate and/or synchrony) for drifting sinusoid gratings versus drifting concentric sinusoid rings.

Analysis of the firing rate suggests that there is not a clear preference for linear contours versus curved contours within our sample. The greatest average firing rate for each cell was chosen across 36 orientations (10° increments) for gratings and 16 center locations for rings. For n = 51 single cells and 631 pairs, the average firing rate is nearly the same for gratings and rings—13.7 ± 1.9 versus 16.2 ± 2.0 sps (t-test; P > 0.18) for the two stimuli, respectively. We would expect to underestimate the activity from rings because we tested a relatively limited number of ring locations and were therefore unable to match the preferred orientations and directions for the entire population. We were, however, able to match the preferred orientation and direction for all 51 cells with gratings. Therefore overall the firing rate alone is inconsistent with the psychophysical data and discourages the notion of an association field organization in primary visual cortex.

Synchrony conversely does appear to show an overall preference for gratings over rings as the behavioral tests suggest. When we include all pairs of cells (n = 47 cells and 188 pairs) that showed significant synchrony (a central peak that was ≥2 times the random fluctuation in the CCH), the preference for gratings is substantial: gratings (collinear) = 0.90 ± 0.06% versus rings (curvilinear) = 0.36 ± 0.04% (t-test; P < 1.3 × 10−12). If we examine only pairs of cells with RFs aligned with the rings contour orientation and direction (n = 47 cells and 127 pairs), the average synchrony for gratings (0.66 ± 0.04%) is still significantly (t-test; P < 5.0 × 10−6) greater than that found for rings (0.40 ± 0.04%). For the same 47 cells, there is still no significant difference in the average firing rate between gratings and rings—14.5 ± 2.0 versus 17.0 ± 2.1 sps (t-test; P > 0.19).

The probability of observing synchrony for a given pair of cells also matches the orientation rule of the association field theory (Fig. 5, left). If the pair of cells has orientation preferences within 30° (n = 185 pairs), the probability of measuring significant synchrony is 80.0% (see also Gray et al. 1989; Samonds et al. 2004; Ts’o et al. 1986). If the pair of cells has orientation preference differences >30°, their RFs are cocircular (e.g., Fig. 1), and the pair was tested with an appropriately aligned ring stimulus (n = 76 pairs), the probability is reduced to 50.0%. Our data are insufficient to explore systematically the relationship between probability of synchrony and orientation preference difference, but clearly the trend matches the prediction. Overall, the change in strength in synchrony and the probability of observing synchrony appear to depend strongly on the relationship of orientation preference between pairs of cells in visual cortex that is consistent with the predictions of the association field model.

Our synchrony data do not at first glance appear to support the proximity rule of association field theory. Across all synchronous pairs (n = 188), the greatest synchrony found for gratings or rings did not covary with respect to average RF overlap or maximum RF overlap (e.g., 100% when the RF of 1 cell is completely within the RF of the other cell): r2 = 0.01 for both measurements.

However, this might be attributed to including only pairs of cells with significant synchrony. Pairs of cells without significant synchrony would essentially have synchrony measurements of zero or near zero. If these pairs tend to have greater distance between their RFs, then the trend with respect to proximity would be stronger. Therefore the proximity rule might be more apparent by measuring the probability of observing synchrony based on RF overlap. Figure 5 (right) illustrates the probability of observing synchrony for three subpopulations of pairs based on average RF overlap (<25%, 25–50%, >50%). For pairs of cells with orientation preferences within 30° (collinear), we do not find any difference among the three groups (all are ~80%). For cocircular pairs (with orientation preferences >30°), the probability of observing synchrony increases with increasing proximity (29.2 to 55.6 to 64.0%) matching the association field prediction.

For any given orientation preference difference, the association field model predicts decreasing probability of integration with respect to distance between segments. The preceding

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1 The Supplementary Material (three figures) for this article is available online at http://jn.physiology.org/cgi/content/full/01070.2005/DC1.
results show this to be true for the probability of synchrony only for cells with >30° differences in preferred orientation. To see if there still might be some support for the proximity rule for orientation preference differences ≤30°, we measured the strength of synchrony with respect to average and maximum RF overlap for the orientation preference difference with both the strongest and most reliable synchrony measurements. Pairs of cells with orientation preferences within ±10° of each other (n = 64 pairs) should have significant synchrony across the entire spectrum of proximity. Even for these pairs, however, the relationship between the strength of synchrony and greater RF proximity (defined as average and maximum RF overlap) is still rather weak (r² = 0.13 and 0.14; Fig. 6, A and B, respectively).

Although we did not find a clear general relationship between synchrony and proximity for probability of observation or magnitude, the trends we did observe were in the right direction. This weak proximity relationship and the progression to larger RFs from striate to extrastriate cortex might suggest that contour integration needs to extend beyond V1.

**Classification based on RF organization**

In the next three sections, we take a closer look at RF relationships and their connection to stimulus contour to characterize how these interactions shape firing rate and synchrony. Based on the relationship between the RF locations and orientation preferences for each cell pair, we classified pairs a priori either as prefers rings (PR) or prefers gratings (PG). PR pairs of cells had cocircular RFs (Fig. 1) so they were predicted to have greater activity for drifting concentric rings versus drifting collinear gratings (Fig. 7A). Collinear pairs are both driven by the same (preferred) orientation with the grating. While the exam-

![FIG. 5. Left: probability calculations of observing synchrony based on the orientation preference of cells. Right: probability calculations of observing synchrony based on the RF overlap of cells (proximity).](http://jn.physiology.org/)

![FIG. 6. Relationship between synchrony and proximity. A: scatter plot of synchrony vs. average RF overlap for pairs of cells with orientation preferences with ±10° of each other (n = 64 pairs). B: same as in A using the maximum RF overlap of 1 cell with respect to the other in each pair.](http://jn.physiology.org/)
ple pair shown in Fig. 7C is driven by nonoptimal grating orientations; with rings of the opposite curvature, orientations are yet more nonoptimal (e.g., orthogonal).

Many cell pairs were unsuitable for this analysis. When RFs have excessive overlap, PG/PR classification is ambiguous (Fig. 7D). Additionally, the most appropriate center location for the rings could not be chosen for each of the 631 pairs—nearly all require a unique location. Because recording time was limited, we chose a limited number of ring centers (see Fig. 3, C and D) selected to maximize our yield of data with an adequate number of samples (100–200 stimulus repetitions). A large portion (81%) of the 631 pairs of cells recorded with the 100-electrode arrays were disqualified for at least one of these two reasons, and these pairs were not subjected to further analysis (see selection criteria details in METHODS).

The remaining sample that we analyze in detail seems representative of our entire population. First, this sample includes 47 of the 51 total cells and the overall firing rates of the two samples are not significantly different ($t$-test; $P > 0.38$ and $P > 0.39$ for gratings and rings, respectively). Second, the fact that we limit our analysis to pairs with significant synchrony does not lead to a small unique sample of cells. If this was true, we might deceptively imply a more dramatic role for synchrony in contour integration merely because we were seeking out synchronous pairs. In fact, choosing synchrony as a selection criterion is nearly the same as explicitly choosing cocircular RF relationships. As shown in the preceding text (see Fig. 5), 71.3% of cocircular (which includes collinear) pairs ($n = 186$ of 261 pairs) have significant synchrony in one of the two stimulus conditions when appropriately matched with the stimulus ($<30\%$ of the sample produces false negatives). We measured significant synchrony in 0.7% of the pairs ($n = 2$ of 307 pairs) that did not have any clear cocircular RF relationships ($<1\%$ of the sample produces false positives).

Each pair of cells that was classified as either PR or PG was assigned a cocircularity value (measured in degrees) calculated as the difference between the cells’ orientation preferences. Cocircularity should not be confused with the definition cocircular described in Fig. 1. All 127 pairs in this population are implicitly cocircular because they are aligned with the rings or gratings stimulus. Cocircularity simply characterizes the degree of curvature for each cocircular pair. Cocircularity was negative for the curvatures opposite those of the stimulus. Greater cocircularity for a cell pair predicts a better match between their RF properties and the rings stimulus (as opposed to the grating stimulus), provided the location of the rings center was appropriate (Fig. 7E). Dashed lines represent the opposite curvature of the rings stimulus (dashed curve) or an inward direction of motion.

**Do the response properties for PR and PG pairs match our predictions?**

We measured the response of cell pairs to rings and to gratings with an orientation that best matched the preferred orientations of the two cells. We would predict (Fig. 7) that the response for PR pairs should be maximized with rings and the response for PG pairs should be maximized with gratings. Figure 8, A—C, shows the synchrony and firing rate statistics for PR pairs of cells. For this group, the rings nearly doubled the synchrony found with gratings (Fig. 8A). As expected, the total average firing rate for this group is also greater for rings versus gratings (Fig. 8C).

Figure 8B shows two cells with an $80\%$ difference in preferred orientation that synchronize for rings and do not syn-
chronize for gratings. In this case, the absence of synchrony for gratings is unsurprising because with a linear grating at the orientation midway between the cells’ preferences, the cells are barely being driven (total average firing rate: 4.9 sps). However, synchrony between two cells with discrete RFs and a difference in orientation preference of 80° is surprising. Synchrony has traditionally been viewed as strictly orientation dependent (Eckhorn et al. 1988; Gray et al. 1989; Ts’o et al. 1986). Counterexamples are sparse with only Das and Gilbert (1999) measuring predictable significant synchrony between cells with differing orientation preferences and discrete RFs for T junction and corner configurations. Castelo-Branco et al. (2000) also found synchrony among cells with differing orientation preferences in areas 18 and PMLS when stimulated by plaid patterns.

The synchrony and firing rate statistics for pairs of cells classified as PG (Fig. 8, D–F) show a pattern complementary to that found with PR pairs. Drifting concentric rings are less effective than drifting gratings at synchronizing these pairs (as predicted). Overall, for PG pairs of cells, synchrony from rings was about a quarter that found with gratings (Fig. 8D). The total average firing rate also decreased for rings versus gratings (Fig. 8F) but considerably less than the change in synchrony (Fig. 8D). Figure 8E shows two cells with the same preferred orientation that generate more synchronization for gratings than for rings. This occurred despite a decrease in the total average firing rate of these two cells from 55.1 sps for rings to 41.3 sps for gratings (contradicting the prediction based on RF organization and orientation preferences).

**Classification based on responses**

Figure 8 suggests that synchrony and firing rate provide essentially the same contour information but that synchrony does so more robustly (Fig. 8, A vs. C and D vs. F). That alone is not very surprising, and it is consistent with past results showing that the spatial acuity (orientation tuning) of synchrony is narrower than that of firing rate (Frien et al. 2000; Samonds et al. 2003, 2004; Snider et al. 1998). The averaged results also suggest that local orientation filtering extends to multiple cells in a straightforward manner.

However, the response difference between rings and gratings contradicting the prediction based on RFs demonstrated in Fig. 8E was not an isolated case, which we will demonstrate in this section. Even though the average statistics across the population of cell pairs imply that synchrony and firing rate provide essentially the same information, on a pair-by-pair basis, the total average firing rate failed much more often than
synchrony in tests of PR and PG predictions. The firing rates of the two cells did not predictably reflect the relationship between the orientations displayed in their RFs and their orientation preferences. Responses to rings were generally higher than responses to gratings despite the latter having a much better match with the orientation tuning of both cells.

To assess the reliability of a given coding scheme, we reclassified each pair of cells as either PR or PG on the basis of either synchrony or total average firing rate (as opposed to RF structure) and compared the results to our original classification described in Fig. 7. For example, if grating stimulation yielded greater synchrony than ring stimulation, we classified pairs as PG and vice versa. The classification errors can then be used to calculate transmitted information (Victor and Purpura 1996). With this simple strategy, synchrony provided 0.40 bits of information, whereas the total average firing rate provided only 0.13 bits of information (the most information possible is 1 bit). Confidence intervals and bias for the information measurements were estimated with the bootstrap method (Efron and Tibshirani 1993), and the difference between synchrony and firing rate information was significant ($\alpha < 0.005$).

Figure 9 shows pair-by-pair results for the response-based (A, synchrony; B, firing rate) classification described in the preceding text. The data for each pair of cells are plotted as the RPI (see METHODS for details), which ranges from $-1$ to 1 and represents the difference in synchrony (for RPIs, Fig. 9A) or firing rate (for RPIf, Fig. 9B) for rings versus gratings divided by the sum of the synchrony or firing rate, respectively (Eq. 1). RPI should vary from $-1$ to 1 with respect to cocircularity (which represents the preference for rings stimulation based on RF relationships). There should also be a slight positive bias for RPI with respect to cocircularity (rightward shift) because zero cocircularity has a preference for gratings stimulation. Open circles in Fig. 9 represent classification errors—i.e., when the response behavior did not match the prediction based on the RF properties. The total average firing rate clearly resulted in more classification errors (more open circles) than the synchrony as illustrated above with the information measurements.

Figure 9 also shows whether RPI varied systematically with cocircularity. One would predict a direct dependence between the two quantities because both quantities are related to the degree of stimulus curvature. The data points should cluster in the lower-left and upper-right quadrants, approaching $-1$ and 1 in the two quadrants with decreasing and increasing cocircularity, respectively. Again, by comparing Fig. 9, A with B, the synchrony clearly outperforms the total average firing rate on a pair-by-pair basis. The data points cluster in the appropriate quadrants in Fig. 9A, whereas the data points appear to be equally scattered around the origin in Fig. 9B. Regression analysis of a sigmoid fit confirms that the synchrony varies systematically with the cocircularity more reliably than the total average firing rate ($R^2 = 0.52$ vs. $R^2 = 0.19$; $\alpha < 0.001$). The best-fit sigmoid for synchrony also matches the expected RP-cocircularity relationship (described in the preceding text) much better than the fit for the total average firing rate. However, both functions at least show the slight positive bias with respect to cocircularity.

**Converging and diverging inputs?**

Even though there was only a slight dependence on RF overlap, we wanted to take a closer look at common input as a possible source of our synchrony. The average receptive field overlap for the entire population with significant synchrony ($n = 188$) was $41.5 \pm 1.6\%$, which was expected because the majority of the significant synchrony that we measured was between electrodes that are within the range of overlapping RFs for area 17 in cats (5 mm$^2$; see Fig. 10) (Albus 1975).

In addition, the lag times of our cross-correlograms support common input as the probable source of synchrony. A large percentage (43%) of the synchrony peaks we measured were at 0 ms, and the average center of the synchrony peaks was displaced only $1.4 \pm 0.2$ ms. Again, this is predicted by the anatomy because electrode pairs yielding synchrony fell within the extent of the most distant projections measured from layer 4 to layers 2/3 in cats (5 mm) (Martin and Whitteridge 1984). We see a clear drop-off in synchronous pairs that lay outside of this region but still within the array dimensions (Fig. 10).

However, within this region where common input is expected we do not see a clear systematic relationship with electrode distance and the strength of synchrony ($n = 188$ pairs; $r^2 = 0.01$; Fig. 10). Our data only weakly suggest that

![Figure 9](http://jn.physiology.org/)

**FIG. 9.** Rings preference index (RPI) vs. cocircularity. A: gain in synchrony (RPIs, Eq. 2) for rings stimulation with respect to gratings stimulation (open circles contradict the prediction based on RF organization). B: gain in the total average firing rate (RPIf, Eq. 2) for rings stimulation with respect to gratings stimulation.
the strength of synchrony decreases with increasing distance between electrodes (Das and Gilbert 1999). However, we were unable to investigate pairs closer than 400 \( \mu \text{m} \) (electrode spacing on the array), which were examined by Das and Gilbert (1999). Figure 6, A and B, also shows that within the 5-mm window there is not a strong systematic relationship between the RF overlap and the strength of synchrony. These two points, together with the observation that 5% of our pairs had wholly separate RFs and >12% of our pairs had <10% overlap, suggest that the synchrony we observe does not simply reflect common inputs. Nonetheless, both the lag times and the physical extent of the interactions suggest that synchrony arises from the bottom-up converging and diverging inputs from earlier levels of the visual system. One explanation for the lack of any clear systematic relationship with anatomy is that the synchrony is dynamic, which we will describe in the following section. Due to the overlap of these converging and diverging inputs, the synchrony cannot be resolved exclusively with a connectionist description of the cortical network.

**Stimulus-dependent dynamic synchrony**

We also examined how synchrony within cell groups larger than pairs depended on the form of stimulation. One theory for cortical representation of information is that cells change their membership within a particular subpopulation (defined by synchrony) as stimuli vary (von der Malsburg 1981). Figure 11 (left) shows the RFs of three cells simultaneously recorded. When a drifting grating is presented, the two cells on the left (red), which are essentially collinear, synchronize, whereas the rightward cell does not synchronize with either of the two on the left (Fig. 11A, middle). When drifting concentric rings are presented, the two cells on the right (blue), which are nearly orthogonal but positioned to prefer this ring stimulus, synchronize, whereas the leftward cell does not synchronize with either of the two cells on the right (Fig. 11B, middle).
The firing rate tuning of the cells (Fig. 11, A and B, right) roughly predicts the groupings for changing stimulation. However, the synchrony is much more precise, acting like a logical AND gate that only allows the stimulus to synchronize the cells at the intersection of the tuning. For collinear contours, the strongest synchrony occurs for the orientation between the two cells’ preferred orientations (Fig. 11A, right, red arrow) and weakens with changes in either direction (green curve is synchrony measurements). We see this behavior consistently across our entire sample, which matches several previous reports (see quantitative description in Ghose et al. 1994; Kohn and Smith 2005; Samonds and Bonds 2005; Samonds et al. 2003, 2004). For curved contours, the rings need to be precisely aligned with both RFs to allow cells with nonoverlapping orientation tuning to synchronize (blue arrows are direction of the ring with respect to each cell’s RF). We again see the synchrony weaken or disappear with changes in the ring center location. However, the number of ring centers that we used was too sparse to characterize systematically the dependency of synchrony with respect to alignment for curved contours.

Figure 12 shows how the example of dynamic grouping in Fig. 11 extends to our entire population of pairs. A scatter plot of all synchrony measurements (Fig. 12A) shows that the strongest synchrony for gratings occurs for cell pairs with zero cocircularity (i.e., strictly collinear), which matches previous reports (Gray et al. 1989; Samonds et al. 2004; Ts’o et al. 1986). The synchrony is both more reliable and more selective than the firing rate at predicting whether a stimulus is collinear (Fig. 12, A vs. B; \( \alpha < 0.005 \)). If synchrony is a general mechanism for contour integration, it must also play a role in detecting cocircular contours. Figure 12C illustrates that ring stimuli tend to shift the strongest synchronization from collinear pairs to pairs with higher cocircularity, synchronizing pairs with differing orientations (note that overall the average synchrony is weaker in Fig. 12, C vs. A). Again, synchrony is more selective and more reliable than firing rate at predicting the stimulus (Fig. 12, C vs. D; \( \alpha < 0.001 \)). The increased selectivity and reliability of the synchrony is not simply a multiplicative result of firing rate probabilities (see Supplemental Materials). The synchrony that we are measuring is above the chance level that is predicted by multiplying firing probabilities (which is in any case subtracted from the measurement) (Aertsen et al. 1989). The Aertsen et al. (1989) rate-normalized synchrony we use, also termed effective connectivity, is clearly dynamic (i.e., not simply a fixed consequence of anatomical connections) and stimulus dependent with respect to contour configuration.

Last we want to comment on the magnitude of the synchronous behavior we observe and its implications with respect to the decoding of contour information by higher visual areas (see details in Supplemental Materials). The synchrony peaks (1-ms bins) among visual cortical pairs are relatively weak (mean <1%; see Fig. 12, A and C). Integrated over a window of 10 ms, the average synchrony (correlation coefficient) is 6.2% (typically <20%). A hypothetical coincidence detector cannot distinguish between synchronous spikes that arise from chance and those that arise from network dynamics and connectivity (Shadlen and Movshon 1999). Based on our average firing rates, the synchronous spikes that arise from chance within a 10-ms window is on average 11.0% (and increases with increasing firing rates). Therefore if we consider the synchrony we are measuring as the contour signal, the firing rate will add a considerable amount of noise. Whether or not this is detrimental to our interpretations described in the following text cannot be determined from our data alone. First, the firing rate information is not all noise. Although more coarsely and with more errors, the firing rate still encodes some contour information (and with a coincidence detector there is some improvement over summing firing rates; see Supplemental Materials). In addition, we cannot determine how the signal-to-noise will
scale over larger numbers of cells although it seems likely that it would increase (Samonds et al. 2004).

**DISCUSSION**

One of the fundamental presumptions about the role of V1 in visual processing is that single-cell orientation tuning forms the foundation for a system that detects edges or contours (e.g., Marr and Hildreth 1980). The association field theory provides rules about how orientation detectors might combine based on natural scene statistics and psychophysical tests of contour detection (Alais and Lorenceau 2002; Elder and Goldberg 2002; Field et al. 1993; Geisler et al. 2001; Pettet 1999; Pettet et al. 1998; Pizlo et al. 1997; Polat and Sagi 1994; Sigman et al. 2001). Lateral connections are thought to be critical in contour integration by enhancing responses to cells with collinear RFs driven by a single contour (Gilbert and Weisel 1989; Gilbert et al. 1996). Evidence of such enhancement (Kapadia et al. 1995) and the anatomical organization of horizontal connections in V1 (Bosking et al. 1997; Gilbert and Weisel 1989; Lund et al. 2003; Malach et al. 1993; Stettler et al. 2002) support this proposal and provide physiologic and anatomic links with the association field model.

**Contextual interactions and contour integration**

The predominance of horizontal connections among cells with similar orientation preferences (Bosking et al. 1997; Gilbert and Weisel 1989; Lund et al. 2003; Malach et al. 1993) would predict greater firing rates for gratings (stimulation of similar orientations) versus rings (stimulation of different orientations) if such connections are facilitatory. However, our results suggest that overall these lateral connections offer no advantage to responses from grating stimulation over concentric rings stimulation because the average firing rates are nearly the same in the two conditions. In addition, we find that aggregate V1 responses to gratings or rings stimulation are not easily predicted from the independent orientation tuning functions (Fig. 9B). The integrated firing rates are ambiguous and are therefore unreliable as encoders of the shape of the contour segment within the local RFs. Contour orientation must not be the only influence on firing rate (see also Hess et al. 2003).

This response ambiguity could result from contextual modulation of V1 responses by stimuli extending beyond the classical RF (CRF) (Fitzpatrick 2000). Although there are some systematic trends (e.g., Kapadia et al. 1995, 2000) for modulation of the CRF response by peripheral stimulation, there are also considerable inconsistencies (Jones et al. 2002). The reported effects include suppression, facilitation, and disinhibition with surround suppression being the most consistent result (Cavanaugh et al. 2002; Guo et al. 2005; Jones et al. 2002; Yao and Li 2002). In most cases, suppression is strongest when the surround stimulus properties match the CRF stimulus properties, which is inconsistent with purely excitatory integration between cells with similar orientation preferences. Facilitation can occur when the surround orientation is orthogonal to CRF orientation, suggesting that contextual modulations might play a role in segmentation (Lamme 1995; Marcus and van Essen 2002; Sillito and Jones 1996). In limited cases (42%), the same orientation in the surround with collinear alignment results in facilitation, suggesting that contextual modulations support contour integration (Kapadia et al. 1995). However, Cavanaugh et al. (2002) suggest that collinear facilitation might be overestimated in Kapadia et al. (1995) due to underestimating the extent of the CRF. Last, surround effects have also been shown to support the integration of discontinuities such as junctions and corners (Sillito et al. 1995).

On the whole, gratings are more likely than rings to cause surround suppression (Jones et al. 2002) because rings distribute energy across a variety of orientations in the surround. Although an optimally oriented grating might generate a greater response from two collinear CRFs, it is reduced by suppression outside the CRF. Surround antagonism is likely less with rings stimulation. Thus although gratings are more effective for the CRF response, rings may ultimately generate an identical or larger firing rate, resulting in ambiguity about the local contour curvature. A similar response ambiguity would also arise with contrast changes (which minimally affect contour integration) (see Hess et al. 2003). Synchronous integration again would preserve the contour information lost in the ambiguous firing rates because contrast leads to negligible changes in synchrony strength (Kohn and Smith 2005; Snider et al. 1998).

We believe that our sample of pairs and choice of stimuli generalize for the behavior of layers 2/3 of V1. Our comparison of firing rate versus synchrony was made when the local stimulus orientation was matched with the RFs of both cells. Our sample of cells was restricted to superficial layers, but the array dimensions (4 × 4 mm) provided us with a widespread sample across multiple orientation columns. Limiting our analysis to synchronous pairs does not appear to bias our sample significantly among this selection of cells. If our source of stimulation (gratings covering 16° of visual angle) biased our sample, it would be toward including more cells enhanced by elongated contours (i.e., not including cells enhanced by discontinuities or cells with strong suppressive surrounds). Our choice of gratings is unlikely to influence our interpretations substantially because the predominance of suppressive surround effects has been found with bars, gratings, and natural scenes (Cavanaugh et al. 2002; Guo et al. 2005; Jones et al. 2002; Yao and Lee 2002).

**Dynamic contour integration**

We propose that contour integration is primarily driven by bottom-up synchronous integration via the diverging and converging anatomy in the earlier stages of visual processing (Alonso et al. 1996; Usrey and Reid 1999). Synchrony is more prominent and predictable than facilitation when tested over a diverse population of cells—i.e., synchrony occurs for >70% of our cocircular pairs (see also Gray et al. 1989; Samonds et al. 2004; Tso et al. 1986) (>75% occurrence for similar orientations), whereas collinear facilitation occurs for less than half of V1 cells (Kapadia et al. 1995) and even that might be an overestimation (see preceding text) (see also Cavanaugh et al. 2002). Overall our data show that both the magnitude and probability of observing synchrony match the fundamental prediction of the association field model: segments are more likely to be part of the same contour when they are similarly oriented. Our analysis of electrode distance, RF overlap, and synchronous lag times all suggest that the synchrony we observe can most simply be explained by common and syn-
chronous input from previous levels of the visual system. Specific afferent projections (100–300 µm) from layer 4 to layers 2/3 can span as much as 5 mm (Martin and Whitteridge 1984), which falls well within the range of all the synchrony we measure with the array (Fig. 10).

Collinear contours would synchronize cells within and across different orientation columns that have the same orientation preference. The most acute curves would likely synchronize pairs located at orientation column discontinuities (i.e., pinwheel centers; Bonhoeffer and Grinvald 1992). Synchrony among cells with large orientation differences and discrete RFs can indeed be found near pinwheel centers (Das and Gilbert 1999).

Our data do not necessarily rule out a role for horizontal connections, but there is no clear evidence (e.g., lag times) to suggest that synchrony is driven by direct mono- or polysynaptic excitatory connections at least among the population of V1 cell pairs that we observed. Nonetheless, the synchrony could be driven laterally by an intermediate common input that we were unable to observe. Horizontal connections within V1 suggest an appealing substrate for contour integration because 60–70% of these connections are between columns of similar orientation preferences (Bosking et al. 1997; Malach et al. 1993; Lund et al. 2003; Stettler et al. 2002) and therefore support the association field viewpoint (see Yen and Finkel 1998). However, Sperry et al. (1955) found virtually no change in performance for cats discriminating global contours after transecting horizontal connections throughout area 17, so this raises some doubt about their role in contour integration being critical. Broad integration might take place at higher levels where RFs are larger.

Extent of V1 contour integration?

Although in general our synchrony data support the association field theory, we did not find clear evidence for its prediction of enhanced synchrony or higher probability of observing synchrony with RF proximity (Figs. 5 and 6; note, however, that any trends we did observe were in the right direction). This could be explained because the synchrony that we found was mainly limited to relatively local processing within the visual field. The total separation of contour segments that stimulated cell pairs was always <10° (∼3 complex cell RFs) (Wilson and Sherman 1976) even though the total spread of RFs and stimulation spanned >16°. The average RF overlap was 35%, and only ∼15% of our pairs were discrete or nearly discrete (<10% overlap). The term “local” must be tempered by the fact that in all cases we were still exploring stimulation extending beyond a single V1 classical RF and the cortical distances between electrodes (∼0.4 mm) suggest that the interactions were at least across different orientation columns.

Alternatively, the global aspects and proximity rule of contour integration might be implemented over multiple layers of the visual system hierarchy and possibly combined with inferential top-down mechanisms (e.g., Elder and Goldberg 2002; Feldman 1997; Geisler et al. 2001). This alternative view seems more likely if synchrony is supported by afferent inputs that limit integration within one layer to cell pairs with overlapping or nearby RFs. This limitation is suggested by the result that the majority of the synchrony we measure is within the cortical area of RF overlap (5 mm²; Fig. 2C) (Albus 1975) despite the array covering 16 mm² of cortex. Top-down connectivity could also be another source of the synchrony we measure (e.g., Sillito et al. 1994), but the connections between V2 to V1 appear to lack the necessary organization to support the association field model (Stettler et al. 2002). Nonetheless the flow of information through the visual hierarchy could still support the association field proximity rules while the level of integration via synchronization in V1 guides the orientation rules.

Integration of V1 responses in extrastriate cortex

Use of the contour information provided by synchrony in primary visual cortex requires that cells at higher levels of the visual system act as synchrony decoders or coincidence detectors. Softky and Koch (1993) have suggested that the irregular firing that is preserved from V1 to area MT is a result of the neurons acting as coincidence detectors. The changes in thresholding measured during normal activity also suggest that cortical cells are likely only to integrate synchronous spikes (Azouz and Gray 2003).

We suggest that the selective response of single cells in extrastriate regions of the Macaque monkey (the medial superior temporal area, V2, and V4) to curvature and cocircular spatiotemporal patterns (Gallant et al. 1993, 1996; Hegdé and Van Essen 2000; Orban et al. 1992; Pasupathy and Connor 2001; Saito et al. 1986; Tanaka and Saito 1989) indicates recovery of information provided by synchronous spikes from striate cortex. The selectivity of V2 cells for corners and T junctions (Hegdé and Van Essen 2000) might also reflect coincidence detection of synchrony driven by these features (Das and Gilbert 1999).

Wilson (1999) has suggested that extrastriate tuning for concentric rings and Glass patterns must originate from forms of integration of the responses from earlier levels of visual processing that are more complex than simple summation. Nonlinear integration via coincidence detection of synchronous spikes at least provides substantial improvement for detecting contour shape and has the capacity to resolve the contour ambiguity present in firing rates. Because orientation discrimination improves substantially when considering the synchrony among larger groups of cells, the accuracy in representing contour configuration would likely continue to improve if we were able to examine more cells encoding the same contour (Samonds et al. 2004).

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