SUPPLEMENTAL MATERIALS

Integration by Multiplication

We also analyzed all of our data with the assumption that the hypothetical integrating cell multiplies the firing rates from outputs of our pairs of cells. The probability of synchronous spikes arising simply by chance is equal to the product of the individual cells' firing probabilities (i.e., see above). A multiplying integrator in effect detects the synchronous spikes that arise from chance. This thus constitutes an alternative view of integration, where neurons could still encode information using the firing rate despite very short time constants (acting as coincidence detectors; e.g., Softky and Koch 1993). The reason we chose to compare the sum of firing rates to synchrony rather than the product in the article is that the sum requires the integrating neuron to perform a completely different function than that required to detect synchrony. Nonetheless, we include the product metric in this section because even though both our synchrony measurements and the product metric provide the same integrator-coincidence detector test, it is important to distinguish whether synchrony is a passive reflectance of firing rates or an additional dimension that encodes stimulus information. Because the product metric also requires a coincidence detector, the data presented below would be combined with our synchrony data rather than representing an alternative framework. Therefore, it is important to examine their relative contributions, both in magnitude and signal-to-noise ratio, with respect to cocircularity. We will note the appropriate figures within the article to make such comparisons.

Figure S1 should be compared with Figure 8 in the article. The magnitude of the product of the firing rates is presented as the rate of spikes that would synchronize within 10 ms of each other by chance. The product rate would effectively scale with changes in the size of the temporal window (e.g., 1 ms window would have 1/10th of the average firing rate) because the peak of the product predictor is relatively broad (e.g., see Aertsen et al. 1989). Figures S1A and S1B correspond to Figures 8A and 8D. Qualitatively, the results are very similar—i.e., multiplication does not differ from summation with respect to the average statistics for our sample. However, multiplication does appear to increase the signal-to-noise ratio, which is expected. An analogy would be squaring the tuning curve, which would sharpen the tuning curve, but would not change the general shape. Therefore, even if we assume that the firing rate carries the relevant contour information, it is still advantageous (with respect to signal-to-noise) for cells receiving the outputs of our cells to act as coincidence detectors.

Although multiplying the firing rates rather than summing the firing rates increases the average signal-to-noise ratio in distinguishing between rings and gratings, multiplication does not remove the errors that occur on a pair-by-pair basis. Figure S2 should be compared to Figure 9. Multiplication does change the RPI polarity with respect to summation for a small number of pairs, but the changes were nearly equal for adding and removing errors. The information (0.15 bits) and RPI fit ($R^2 = 0.28$) were not significantly different between multiplying and summing firing rates (Figure 9B), which are both substan-

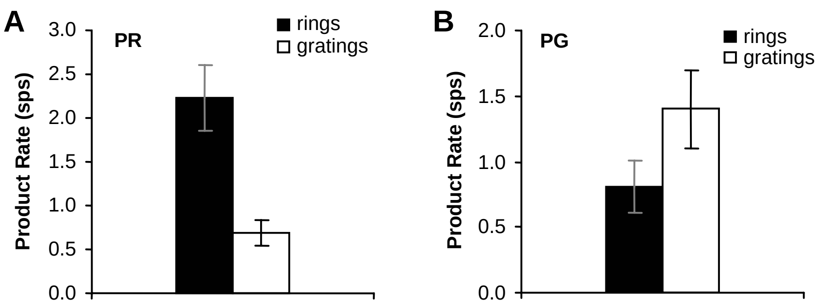

FIG. S1. Activity of PR Pairs vs. PG Pairs. (A) Average product firing rate for all 51 PR pairs for rings and gratings stimuli (standard error bars). (B) Average product firing rate for all 76 PG pairs for rings and gratings stimuli.

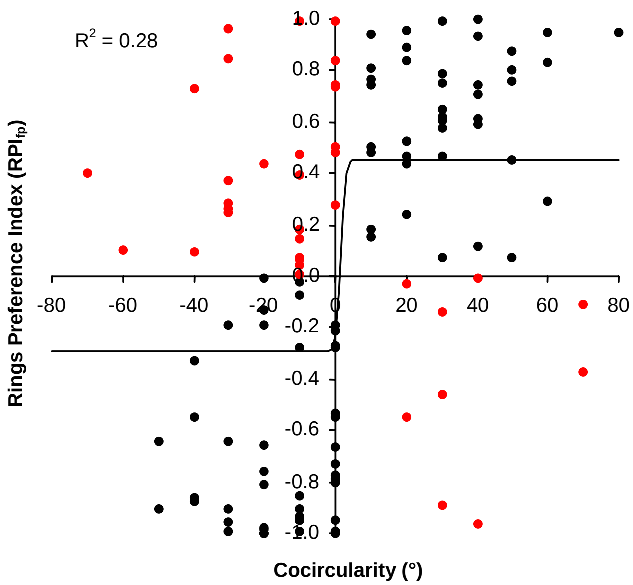

FIG. S2. The gain in the average product firing rate (RPI_{fp}, equation 1) for rings stimulation with respect to gratings stimulation.

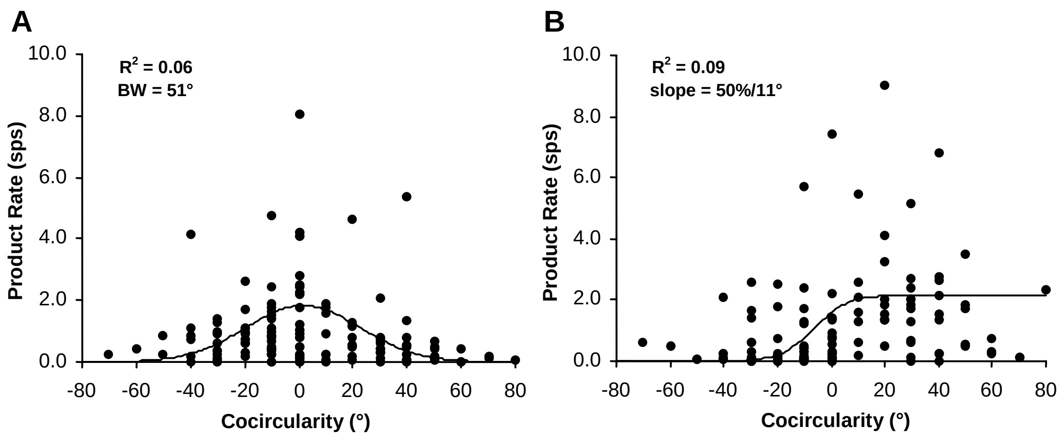

FIG. S3. (A) Product firing rate measurements for N = 127 pairs during drifting grating stimulation. BW = half-height half-bandwidth. (B) Product firing rate measurements for the same 127 pairs of cells during concentric rings stimulation. (slope at 50% magnitude)

tially less than synchrony (Figure 9A).

A scatter plot of the product firing rates versus cocircularity for gratings and rings stimulation (Figures S3A and S3B, respectively) qualitatively falls somewhere between the respective plots in Figure 12 for total average firing rate and synchrony. As mentioned above, the product effectively sharpens the tuning for cocircularity with respect to the total firing rate, which matches the effect of synchrony (Figures 12A and 12C). The reliability (based on regression analysis) though corresponds more closely to the total firing rate (Figures 12B and 12D). Therefore, based on all of our additional analysis the synchrony appears to be distinct from the product of the firing rates (r^2 = 0.16) and the firing rate in general regardless whether the receiving cell acts as an integrator or a coincidence detector. Although both synchrony and the product of the firing rates sharpen orientation tuning, this does not automatically translate into better contour integration and detection.

We can also make a rough comparison of the magnitude of synchronous spikes from chance (Figure S1 or the cross-product predictor) to the magnitude of synchronous spikes beyond chance (CCH). This comparison is inexact because the two values are normalized differently, but offers some perspective. We can compare the rate of the product spikes $\langle x(t_1)\rangle\langle y(t_2)\rangle$ to the firing rates $x(t_1)$ and $y(t_2)$ of the two cells with:

$$C_p = 100\% \frac{\langle x(t_1)\rangle\langle y(t_2)\rangle}{\sqrt{x(t_1) * y(t_2)}} \qquad \text{(S1)}$$

Integrated over a 10-ms window of lag times, on average those pairs that were matched with the appropriate stimulus had C_p = 11.0% (e.g., compare Figure S1 to Figure 8). If we take the area under the CCHs from -5 to +5 ms lag times, the average synchrony is 6.2%. This means the synchrony from chance and the synchrony beyond chance are on the same order of magnitude. Because a coincidence detector will detect both types of synchronous spikes, the firing rate and synchrony can mutually facilitate each other in integration when both are tuned for curvature. However, in those cases where the firing rate (via multiplication) does not encode the contour information correctly (i.e., red points in Figure S2), the firing rate ends up reducing the effective signal-to-noise of the overall synchrony. This is a critical point since the two forms of synchrony are on the same order of magnitude. One way to increase the signal-to-noise ratio in these cases is to reduce the time constant of the integrating cell. The width of the normalized CCH peak is much narrower than the peak of the cross-product predictor (e.g., see Aertsen et al. 1989). For example, if the time constant were reduced from 10 ms to 1 ms, the average synchrony from chance would be ~1.1% and the average synchrony beyond chance would be ~0.8%.

In both cases where we assume the integrating cell acts as a coincidence detector, the selectivity for curvature increases (Figures 8, 12, S1, and S3). However, just passively transforming the firing rate to synchrony via a coincidence detector does not resolve the ambiguity problem of the firing rate in encoding contour information (Figure S2). Synchronous spikes that occur beyond chance begin to resolve the ambiguity (Figure 9A) and provide an additional dimension to encode visual information that does not necessarily have to be in conflict with a firing rate coding scheme. A dynamic time constant, which some recent studies have suggested (Koch et al. 1996; Masuda and Aihara 2002; Azouz and Gray 2003; Rudolph and Destexhe 2003), can transition the receiving cell among these three integration schemes to encode different aspects of the incoming visual information. Because the synchrony from chance can reduce the signal-to-noise ratio of the overall synchrony and is on the same order of magnitude as the synchrony beyond chance, there likely needs to be an element in addition to the time constant that could increase signal-to-noise ratio. The relationship between the two forms of synchrony likely also changes with larger numbers of cells in the sample, which could increase the overall ability of the coincidence detector to decode contour information (e.g., Samonds et al. 2004).

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