APPENDIX

The changes in synchrony we observe can be caused by two factors: a true stimulus dependence due to the fact that different stimuli will provide different amounts of common input to a pair of cells; and a general rate dependence arising from the fact that the apparent strength of synchrony caused by a fixed common input depends on the firing rate of cells. To distinguish between these factors, we have compared two stimulus manipulations that evoke the same firing rate. Because ineffective orientations result in weaker synchrony that optimal stimuli of low contrast that evoke the same firing rate, we conclude that synchrony in V1 is truly stimulus dependent. In an attempt to correct for the general sensitivity of the CCG to changes in firing rate, we scaled the shift-corrected CCG by the geometric mean firing rate of the two cells. While this normalization is frequently used, it is not guaranteed to eliminate the dependence of synchrony on firing rate. It is thus important to determine how the change in synchrony strength we observe depends on the normalization factor we chose, and to test whether other forms of normalization would alter any of our basic conclusions. The different effect of stimulus orientation and contrast on CCG peak width—namely the wide CCG peaks seen at low contrast—is of course independent of any scaling factor.

Consider a reformulation of our equation for the CCG (equation 4):

$$CCG = \frac{CCG_{RAW} - SHIFT}{(\lambda_1 \lambda_2)^n} \tag{12}$$

where the numerator is that of equation (4); λ_1 and λ_2 are the firing rates of cell 1 and 2, respectively; and where we have dropped the correction for trial length since this simply adds a rate independent scaling factor. The exponent, n, determines the strength of the normalization. In Figure 13, we plot the ratio of the CCG peak height (least effective vs. most effective orientation; thin line) as a function of n. Similarly, we plot the ratio of CCG peak height for the low contrast stimulus that evokes a firing rate most similar to that of the least effective orientation and the high contrast stimulus (thick line).

Figure 13A shows clearly that the CCG peak height ratio for both the orientation and contrast data depends critically on the normalization used: the ratio varies almost 100-fold depending on the value of n. When n is zero, for instance, there is no normalization and the CCGs are simply the covariance of counts across trials. In this case, the CCG peak height for both contrast and orientation is much lower for ineffective than effective stimuli (ratio much less than 1). In our study we used an exponent of 0.5, which results in a ratio of roughly 0.4 for the orientation data (60% decrease in peak height) and 0.7 for the contrast data, as in Figure 10. An alternative method for choosing the normalization factor is to plot the logarithm of the peak

height vs. the logarithm of the product of the spike rates *across* pairs, as shown in Figure 13B (Kruger and Aiple, 1988). The slope of this line is the exponent which removes the rate dependence of CCG peak height across pairs; for our data, this exponent is 0.71. Applying this normalization to the *within* pair comparison between stimulus conditions reveals a significant increase in CCG peak height when contrast is lowered (average ratio of 1.37 in Figure 13A; p=0.007) and a significant decrease for the ineffective orientation (average ratio of 0.73; p=0.018). Finally, when the exponent is set to 1 the normalization factor is the product of spike rates and both the orientation and contrast data show an increase in synchrony strength as the stimulus becomes less effective.

Several features of this analysis deserve comment. First, the slopes of the lines for the contrast and orientation data are slightly different. This simply reflects that the ratio of firing rates is slightly higher for the orientation data, resulting in a steeper slope. Had we matched the rates exactly, the lines in Figure 13A would have been perfectly parallel. Second, the absolute change in synchrony clearly depends on the normalization factor used. Since the normalization which removes the general rate dependence is unknown, it is difficult to conclude exactly how the amount of common input is affected by changes in stimulus drive. Instead, we must rely on comparing the relative change in synchrony for different stimulus conditions. Critical for our conclusions, the ratios for the contrast data are higher than for the orientation data, regardless of the normalization used. Thus our conclusion that the strength of synchrony is more sensitive to changes in stimulus orientation than contrast is independent of the normalization used, as long as the two manipulations are normalized by the same factor. Of course, if different stimulus manipulations require different normalization it becomes impossible to compare synchrony across conditions. Our conclusion that altering stimulus orientation and contrast affect synchrony differently relies on the assumption that the CCG should be normalized similarly for these two manipulations, an assumption inherent to all studies that compare synchrony for different stimuli.

Given that the change in CCG peak height depends on the normalization used, it is reasonable to ask why we observed a close relationship between the change in spike timing correlation and spike count correlation (as measured by either r_{CCG} or r_{SC}). Had we chosen to normalize the CCGs by the product of the spike rates, for instance, we would have predicted that the stimulus dependence of synchrony would lead to an increase in r_{SC} on short time scales for both ineffective orientations and low contrast stimuli. The consistency between our two metrics is due to the well-known relationship between spike count mean and variance, as illustrated for our orientation data in Figure 13C. Our normalization of the CCGs by the spike rates is multiplied by the trial length in (4), making the true normalization by the geometric mean of the

spike counts. Our measure of spike count correlation—r_{sc}—is normalized by the variance of the spike count. Since spike count variance is a nearly constant multiple of count mean (Tolhurst et al., 1983; Vogels et al., 1989), these two forms of normalization result in a consistent stimulus dependence of spike timing and spike count metrics. This is a strong motivation for our choice of normalization: it allows one to compare directly these two forms of correlation.
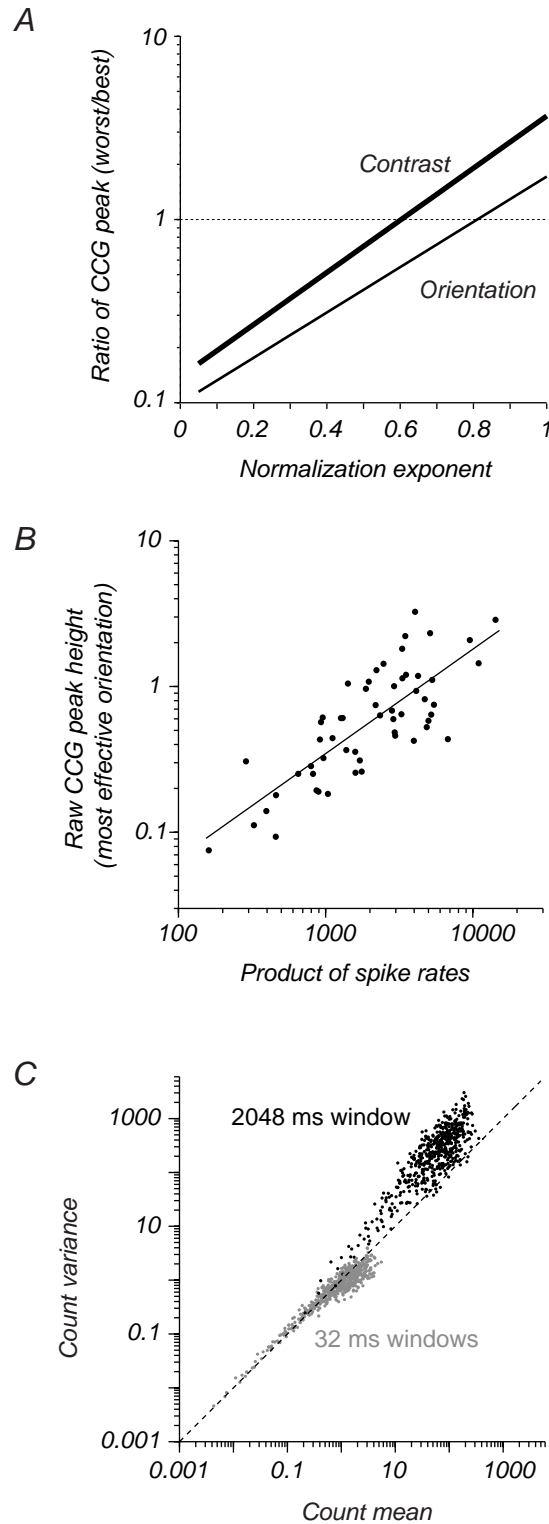
Figure 13: (A) Relationship between CCG peak height ratios and the normalization factor. Orientation data (least effective orientation vs. most effective) is shown with the thin line; contrast data (low contrast vs. high) is shown with the thick line. The stimulus dependence of synchrony depends on the normalization used, but that stimulus contrast and orientation affect synchrony differently does not. (B) Relationship between raw CCG peak height and geometric mean firing rate across V1 pairs. The slope of the line (0.71) is the exponent which removes the dependence on rate (r=0.79; p<0.001). (C) Relationship between spike count variance and count mean for the orientation data set, using two analysis windows: 2048 ms (black) and 32 ms (gray). Each point represent data from one cell and one stimulus condition; there are thus 5 points for each cell.