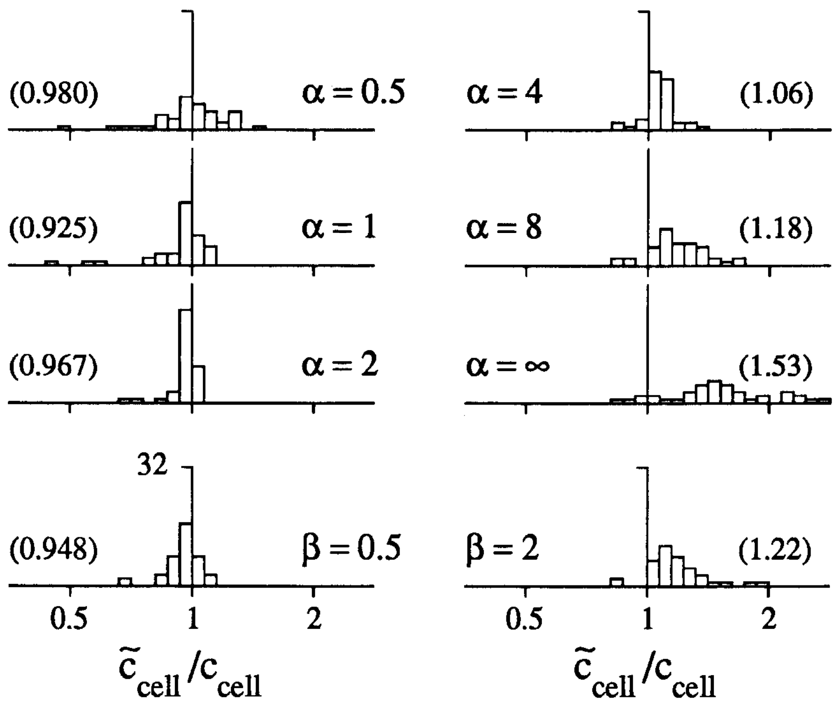

Figure 9. Comparing neuronal thresholds based on spike rate to those based on weighted event counts. For 41 burst cells ($p \geq 1.5$), frequency histograms show the threshold ratio of $\tilde{c}_{cell}$ to c_{cell}. In the *upper six histograms*, $\tilde{c}_{cell}$ is computed from ROC analysis based on the number of single spikes plus α times the number of bursts. The greatest leftward shift in the distribution (*numbers in parentheses* show means), representing the largest average improvement in neuronal threshold, is achieved for $\alpha = 1$, which corresponds to using $\mu_N(c)$, event count, as the neuronal signal. (The counts near 0.5 indicate cells for which the neuronal thresholds were roughly halved by this procedure.) For $2 \leq \alpha \leq 3$, this procedure is very similar to counting individual spikes, since bursts are composed of typically two or three spikes. Histograms for $\alpha = 0.75$, 1.5, and 3.0 (not shown) have means 0.944, 0.940, and 1.02, respectively. As $\alpha \rightarrow \infty$, single spikes are ignored and only bursts are counted. The *bottom two histograms* show results from two schemes that weight events based on the number of spikes per event raised to the power β. The square root yields an improvement in threshold since it reduces the effect of variance in the number of spikes per event, while squaring emphasizes the variance, and worsens the thresholds. Overall, these plots indicate that an ideal observer with knowledge of the arrangement of spikes in bursts will be better able to predict the direction of motion, particularly at near-zero coherence levels, than an observer knowing only the total number of spikes.

between bursts and isolated spikes, we tried various schemes for weighting the contribution of events to the output signal based on a function of the number of spikes per event. First, we weighted isolated spikes, that is, single-spike events, as 1 and bursts, events of multiple spikes, as α, with α varying between 0.5 and 8. We also used a different weighting scheme, where each event, irrespective of whether burst or isolated spike, is weighted according to its number of spikes raised to a power, β. Note that $\beta = 0$ corresponds to the first weighting scheme with $\alpha = 1$, and $\beta = 1$ corresponds to our original scheme, which does not differentiate between bursts and isolated spikes. In addition, we consider $\beta = \frac{1}{2}$ and $\beta = 2$.

To assess the advantage of these schemes, we recomputed neuronal thresholds based on the modified output signals for the 41 burst cells where the peak in the power spectrum was at least 50% above the baseline ($p \geq 1.5$). More weakly bursting cells are ignored because we expect no effect when isolated spikes greatly outnumber bursts. Figure 9 shows the frequency histogram of $\tilde{c}_{cell}/c_{cell}$, where $\tilde{c}_{cell}$ is the neuronal threshold based on the modified signal. The shifts of the distributions are significant ($p < 0.05$) for all histograms shown except for $\alpha = 0.5$. Leftward shifts indicate that the thresholds improved (became lower) when the modified signal was used in place of spike count. The greatest improvement occurred for $\alpha = 1$ (i.e., $\beta = 0$) and corresponds to a 7.5% decrease in threshold. For three cells, thresholds were roughly cut in half. In other words, allowing an ideal observer to count bursts as single events enhances his ability to predict the direction of motion of the stimulus, on average.

Weighting bursts more heavily ($\alpha > 1$) or less heavily ($\alpha = 0.5$) than single spikes did not improve thresholds. Squaring the number of spikes within the burst also led to higher (worse) thresholds, while taking the square root yielded an improvement.

Based on these results, and on the relative variance-to-mean ratios for event count and spike count seen in Figure 8, we believe that the improvement, particularly for $\alpha = 1$, is due to a reduction in relative variance that occurs by ignoring the number of spikes within events. This effect is easily demonstrated by a simple stochastic model. Consider the model that a bursty spike train is governed by two distributions, that of the number of events N and that of the number of spikes per event X. Assume that N is Poisson distributed with rate parameter $\mu_N(c)$, a function of stimulus coherence, and that X is distributed with mean μ_X and variance σ_X^2. Using basic results from the theory of branching processes (Feller, 1968), the mean of S, the number of spikes per trial, is then

$$\mu_S(c) = \mu_N(c)\mu_X, \tag{5}$$

and the variance (see Appendix for proof) is

$$\sigma_S^2(c) = \mu_N(c)(\mu_X^2 + \sigma_X^2), \tag{6}$$

where we use the fact that $\mu_N(c)$ is both the mean and variance