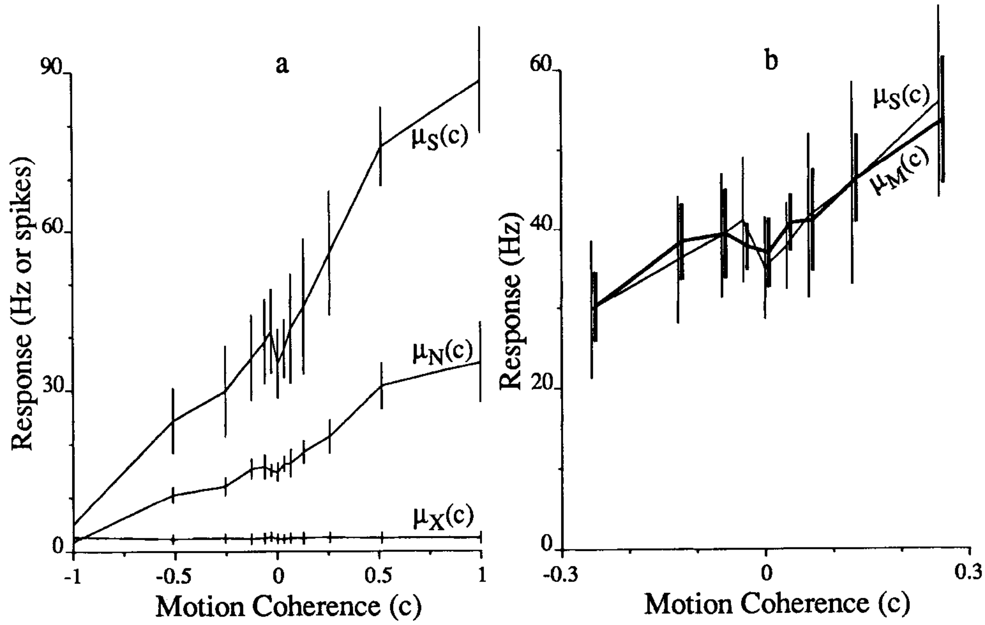

Figure 8. One example of how counting events rather than spikes can yield better direction discrimination. Events are defined to be either isolated spikes or bursts (groups of spikes with all intervals ≤3 msec). *a*, The tuning of mean spike rate [$\mu_S(c)$], mean event rate [$\mu_N(c)$], and the number of spikes per event [$\mu_X(c)$] is plotted relative to motion coherence for the strongly bursting cell *j001*. $\mu_S(c)$ and $\mu_N(c)$ are tuned with *c*, but $\mu_X(c)$ is flat at about 2.5 and is treated as a constant, μ_X, in the text. *b*, Focusing on the region around $c = 0$, $\mu_S(c)$ (*thin line*) is plotted against $\mu_M(c)$ (*thick line, offset*), computed by multiplying $\mu_N(c)$ from *a* by $\mu_X = 2.5$ spikes/event. It is apparent by the smaller SDs and similar slope that $\mu_M(c)$, and thus event rate, is a better basis for predicting *c* than is raw spike rate. Error bars show SDs.

the spike train, *P*, would be similarly correlated with performance.

As in the prior analysis, we eliminated the influence of the visual stimulus itself on the monkey's decisions by carrying out the analysis only for $c = 0$ (completely random motion) and other small coherence levels for which neither the monkey nor the neuron discriminated the direction of motion at levels greater than chance (effectively random motion). On these trials, the monkey "guessed" the correct direction since the visual stimulus itself contained no effective information about the correct choice. For each cell we computed the difference between the average value of *P* for trials on which the monkey decided in favor of the neuron's preferred direction and the average value of *P* when the monkey decided in favor of the null direction. We found no statistically significant difference in *P* between these two conditions for either burst or nonburst cells (paired *t* test, $p > 0.05$), and we therefore conclude that the prominence of the spectral peak in our data set and for our stimulus conditions is not related to the monkey's behavioral choice.

We found a similar result when testing whether *P* was correlated with correct versus incorrect decisions by the monkey at the coherence level closest to the monkey's psychophysical threshold, c_{system} (typically at $c = 0.128$). At this level, there are a significant number of incorrect response trials, and yet the monkey is not simply guessing. Again, we found no statistically significant difference (paired *t* test, $p > 0.05$) for either burst or nonburst cells, and therefore conclude that the prominence of the spectral peak is not related to correct and incorrect responses by the monkey.

Since it is a widely held belief that changes in temporal structure (such as an increase in burstiness) can result from cell damage caused by the electrode, we tested for a change in *P* from trial to trial over the course of the experiment. We found that 13% of burst cells showed a significant increase in *P*, 67% on average, during the experiment, while 12% showed a significant but small (only 8% on average) decrease in *P*. Among nonburst cells, 20% showed a significant increase, while 18% showed a significant decrease in *P*. The magnitudes of the increase and decrease among the nonburst cells were both 10% on average.

Treating bursts as events

We previously appealed to the neuronal threshold, c_{cell}, as a measure of an ideal observer's ability to decide the direction of motion of the stimulus based on the output of the neuron (Newsome et al., 1989a; Britten et al., 1992), assuming that the relevant neuronal output is the number of spikes fired during the stimulus period without considering whether those spikes occurred in bursts or as isolated action potentials. What happens if we quantify the neuron's output by the number of "events," where an event is either a burst or an isolated spike, and recompute an associated neuronal threshold, $\tilde{c}_{cell}$? One could well argue on biophysical grounds that a burst of spikes could be more powerful in evoking a postsynaptic response than the same number of isolated spikes.

Consistent with our definition of *B*, events are defined as the longest sequences of spikes with all ISIs less than or equal to 3 msec (values between 3 and 8 msec give very similar results). With this definition, single isolated spikes as well as bursts are counted as individual events. A nonburst cell will have nearly the same number of events as spikes, while a burst cell will have many fewer events than spikes. Figure 8*a* compares the tuning of a strongly bursting cell's response measured in spikes/second (upper curve), events/second (middle curve), and spikes/event (lower curve). Typical of our database, spikes/event is not tuned with *c*; therefore, the curve for events is similar to that for spikes, but scaled down by the average number of spikes per event, here 2.5. In Figure 8*b*, the thick line shows the events/second curve scaled up by 2.5 spikes/event so that it overlays the spikes/second curve. From the relatively smaller SDs for normalized events/second, it is clear that for this cell events/second is a more useful neuronal signal for predicting the direction of coherent motion.

Because the neuronal code that carries motion information in cortex is not known, and since likewise we do not know whether neurons postsynaptic to the one recorded differentiate