**TABLE 1**

Models for connecting the spike count to the exactly-timed spike patterns

| Model | Method | Interval distribution | PSTH matched | Spike count variance | Match precise timing |
|---|---|---|---|---|---|
| Homogeneous Poisson | Uniform Poisson process | | | − | |
| Interspike interval matched | Shuffle interspike intervals | + | | + | − |
| PSTH matched Poisson (non homogeneous) | Time varying Poisson process | − | + | | − |
| Spike count matched | Same as above with trials selected to match spike count | + | + | + | + |

**An Accurate Model of Spike Timing**

To account for the results of the information theoretical analyses summarized above, Oram et al (1999) created and tested a new statistical model, the spike count matched model described below. The spike count matched model generates single spike trains in a manner similar to the nonhomogeneous Poisson process that was used by Lestienne et al (1986). Instead of assuming that the process generating spikes was Poisson, however, which would lead to a Poisson spike count distribution, the spike counts were forced to match those observed in the experimental data because, as pointed out above, the Poisson distribution fits the data poorly. If, for example, the data had six spikes in a trial, an artificial train with six spikes was generated (Fig. 4).

Recently Berry and Meister (1998) have shown that the interspike interval distribution affects how well the response can be modeled. Therefore, in the spike count matched and the nonhomogeneous Poisson models, the interspike interval distribution, generated initially by the model, was forced to match that from the data by adjusting the probabilities of the first two intervals. When generated creating a 1 or 2 ms interval, a spike was discarded randomly so that the resulting interval distribution matched the distribution in the data (see Oram et al, 1999). This adjustment of the interspike intervals had a small but significant effect on the numbers of repeating triplets. For example, in V1 the number of repeating triplets averaged 0.57; the predictions were 0.45 for the NHPP model, 0.55 for the spike count matched model, and 0.57 for the spike count matched model with the ISI's adjusted. For the data presented here, only the first two intervals must be adjusted.

Figure 5A shows that the homogeneous Poisson model, the interval shuffling model, and the nonhomogeneous Poisson model all underestimate the number of triplets found in the data. In contrast, the spike count matched model predicts numbers of triplets that are indistinguishable from the numbers found in the data. Because the number of triplets is a stochastic consequence of the spike count and interval distributions and the PSTH, it can carry only information already available from those measures.

Investigating whether particular types of triplets, namely, those defined by particular pairs of intervals, carry additional stimulus-related information is still necessary. Because the number of triplets being counted is large (here the 625 different triplet types with both intervals ≤ 75 ms), a problem arises with multiple comparisons. Even if the spike count matched model is correct, $0.05 \times 625 = 31.25$ tests are expected to be significant at the $p < 0.05$ level. In 10,000 simulated runs of the spike count matched model,