Precisely timed spike patterns in TE neurons recorded during sequential match-to-sample are predicted by a simple stochastic model using the peristimulus time histogram and spike count distribution

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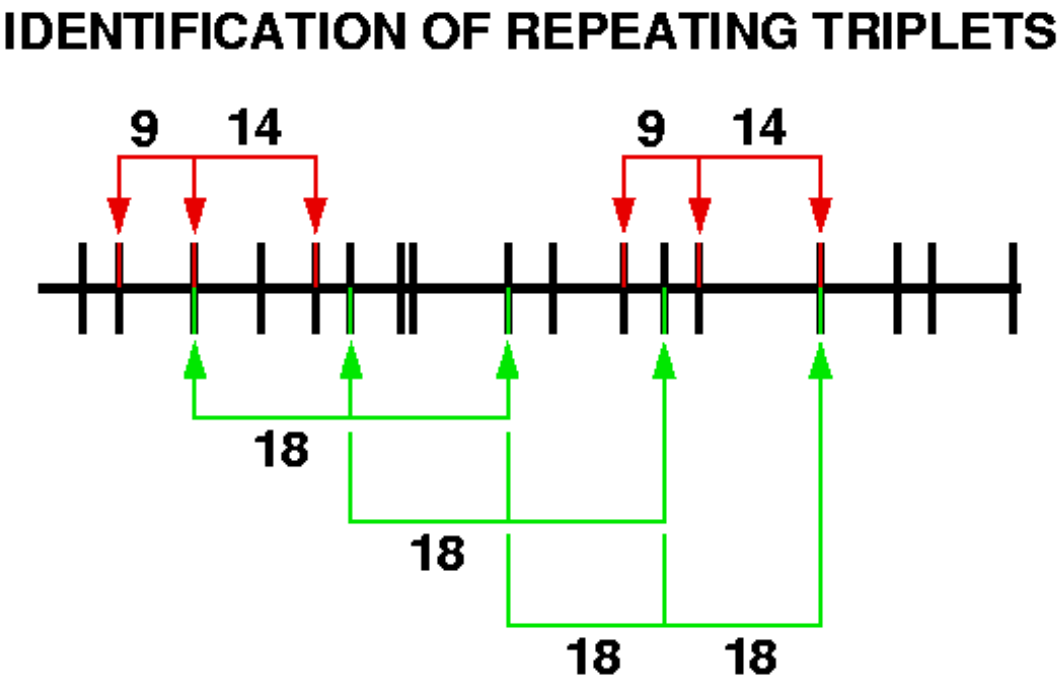
Introduction

Precise times of individual spikes as a method for carrying information has been associated with many psychological phenomena, including binding or linking of different stimulus attributes to form a coherent whole, behavioral relevance of stimuli, decision making processes and even consciousness. Central to the thesis that precise temporal structures in neural responses are associated with neural processing is the idea that they carry information unavailable from coarse temporal response measures. In a previous study of V1 and LGN, repeating triplets carried only information that was redundant with the information carried by spike count when the animal was not required to make behavioral judgements (Oram et al. *J Neurophysiol.* 1999).

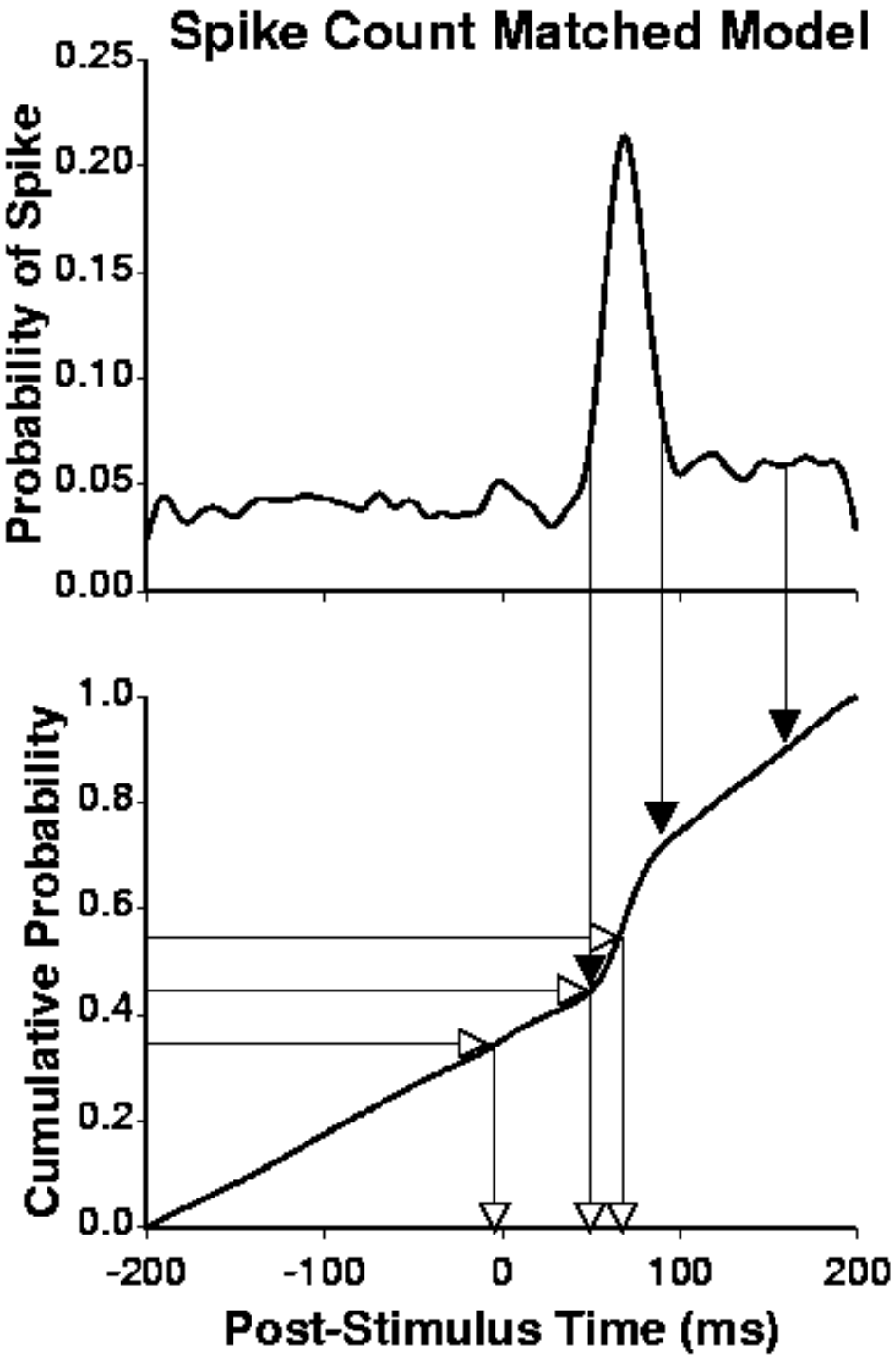
Given the proposed roles of precisely timed spikes in behavioral tasks we report here on the precisely timed spike patterns within the responses of single inferior temporal cortical (area TE) neurons while the monkey performed a sequential delayed match to sample (DMS) task.

Methods

The monkeys performed a sequential delayed match to sample (DMS) task. Stimuli were presented as a sample, with 1-3 non-match stimuli followed by the rewarded match stimulus. Recordings were made from TE neurons while the monkey maintained fixation.

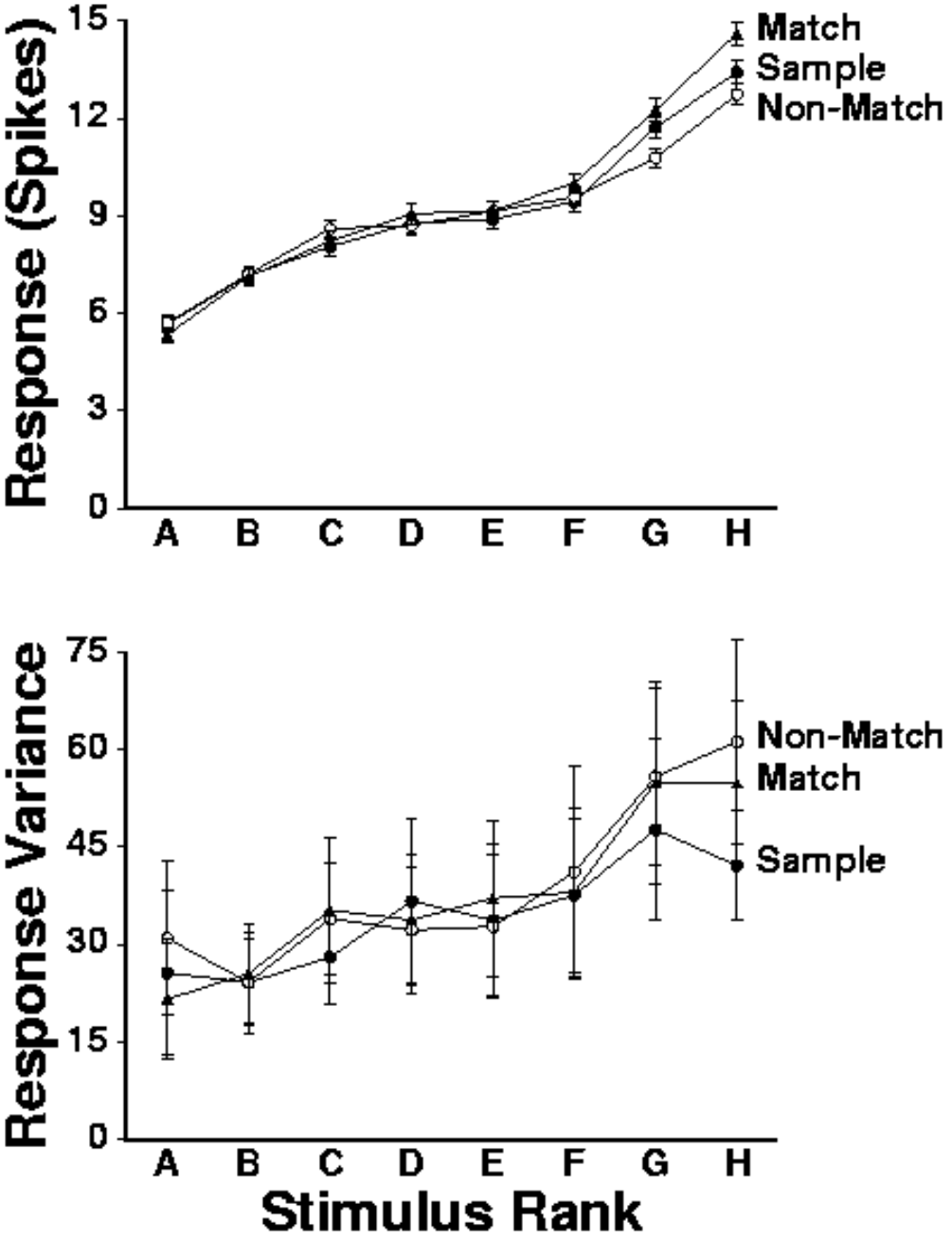


We identified precise patterns of triplets of spikes that repeated within single responses of a TE neuron. We calculated the information carried by the total spike count, the number of repeating triplets and a joint code of both the total spike count and the number of repeating triplets using a well validated artificial neural network (Kjaer et al. *J. Comput Neurosci* 1994).

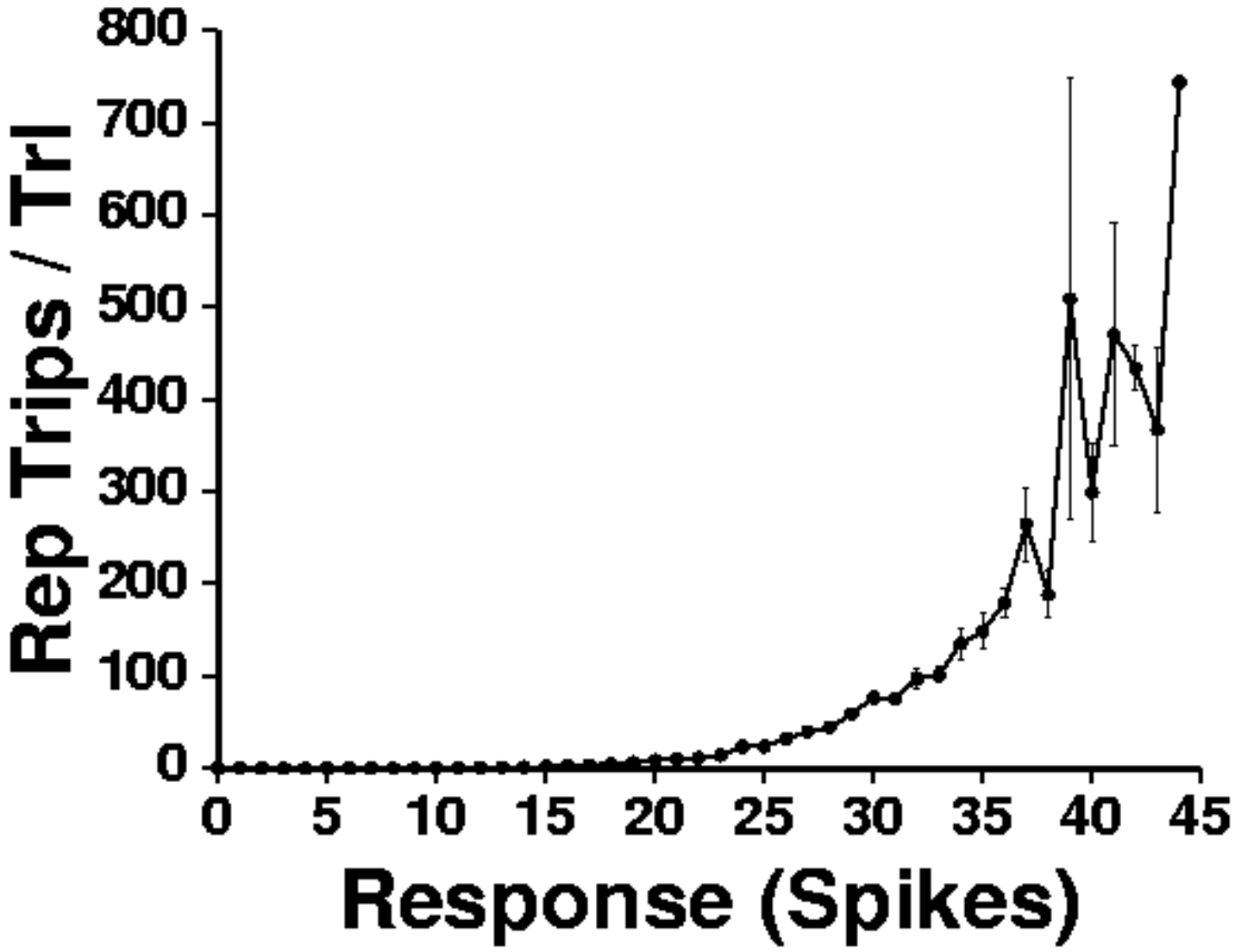


The spike count matched (SCM) model was used to determine the expected number of precisely timed spike patterns within responses (Figure 2). Briefly, the SCM model matches the spike count variance, the inter-spike intervals and the slow time varying PSTH to generate artificial spike trains with stochastic times assigned to each spike (Oram et al. *J. Neurophysiol.* 1999).

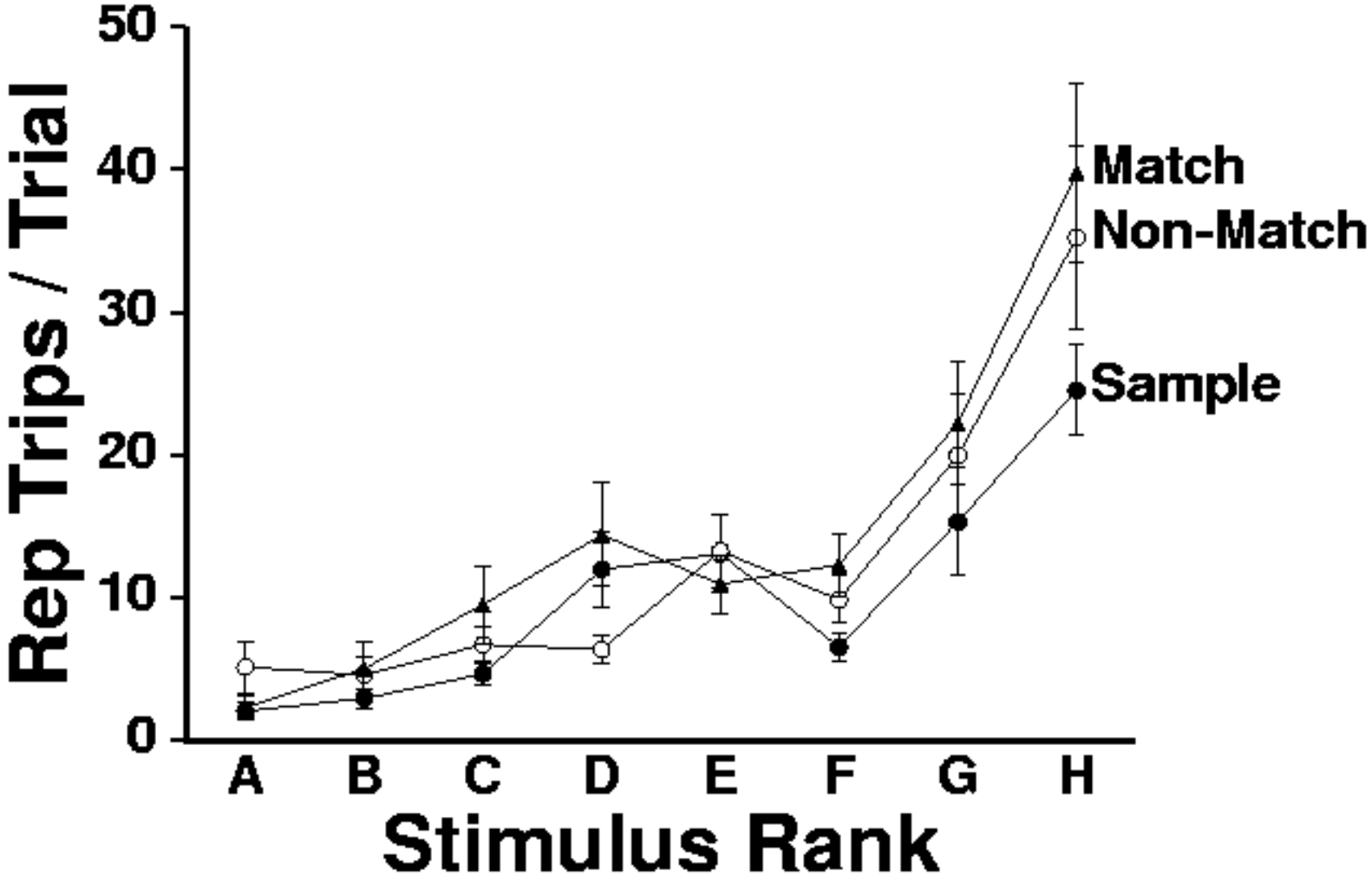
Results



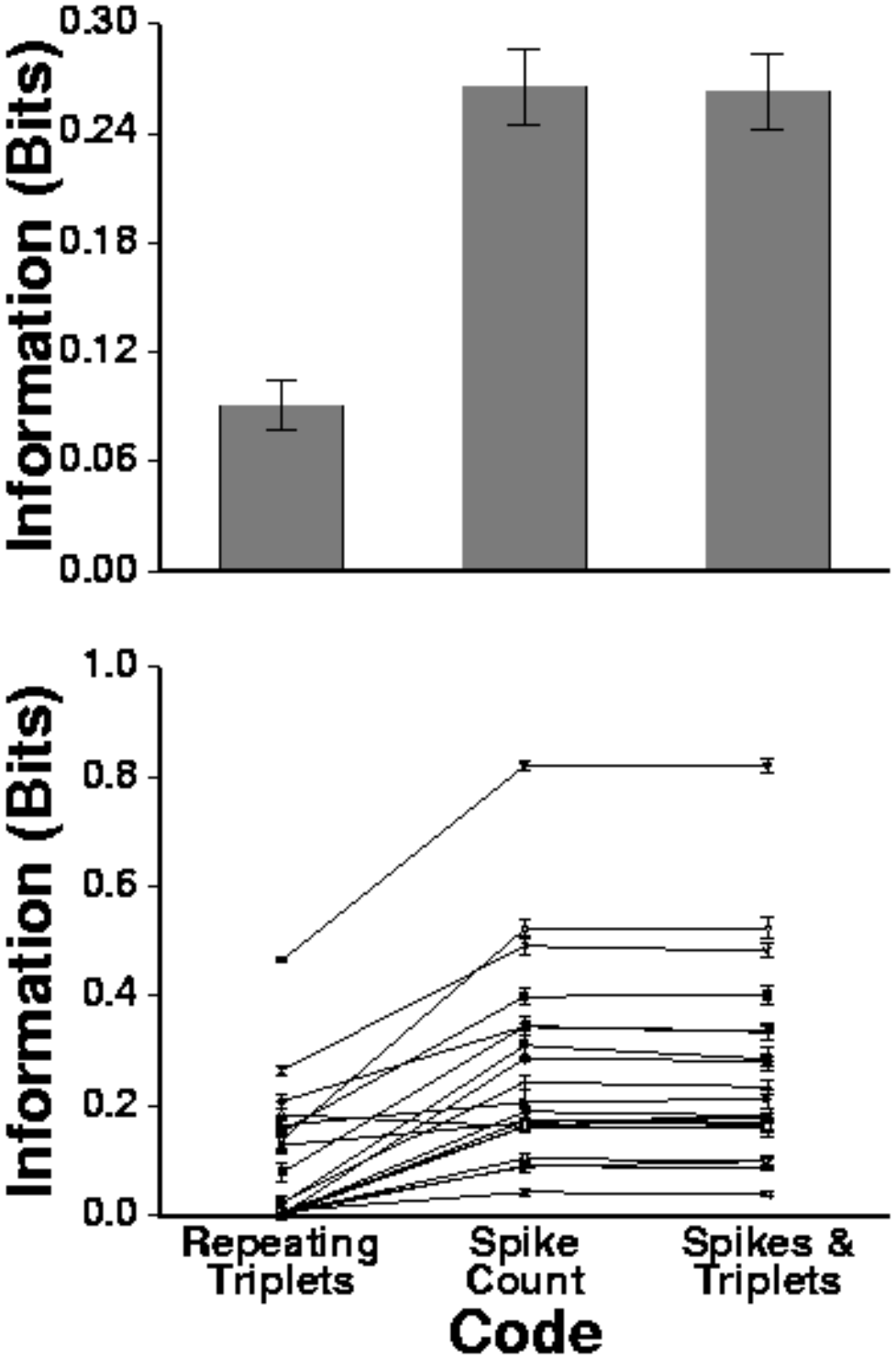
As expected, the behavioral relevance of visual stimuli influences TE activity. Activity from 20 neurons was recorded while the monkeys performed the DMS task. The stimuli were ranked for each cell according to the strength of the responses. Stronger responses of recorded neurons were modulated by the behavioral task. For stimuli which elicited large responses there was an increase in activity associated with presentation of a stimulus as a match compared to the activity when the same stimulus was presented as the sample or as a non-match (Figure 3, upper). Despite the responses to the match stimuli having a greater mean activity, the variance of the responses to stimuli presented during the non-match phase was higher than when the same stimuli were presented during the sample or the match phase (Figure 3, lower). The effect of the behavioral relevance on the response variance was most pronounced for stimuli that elicited large responses.



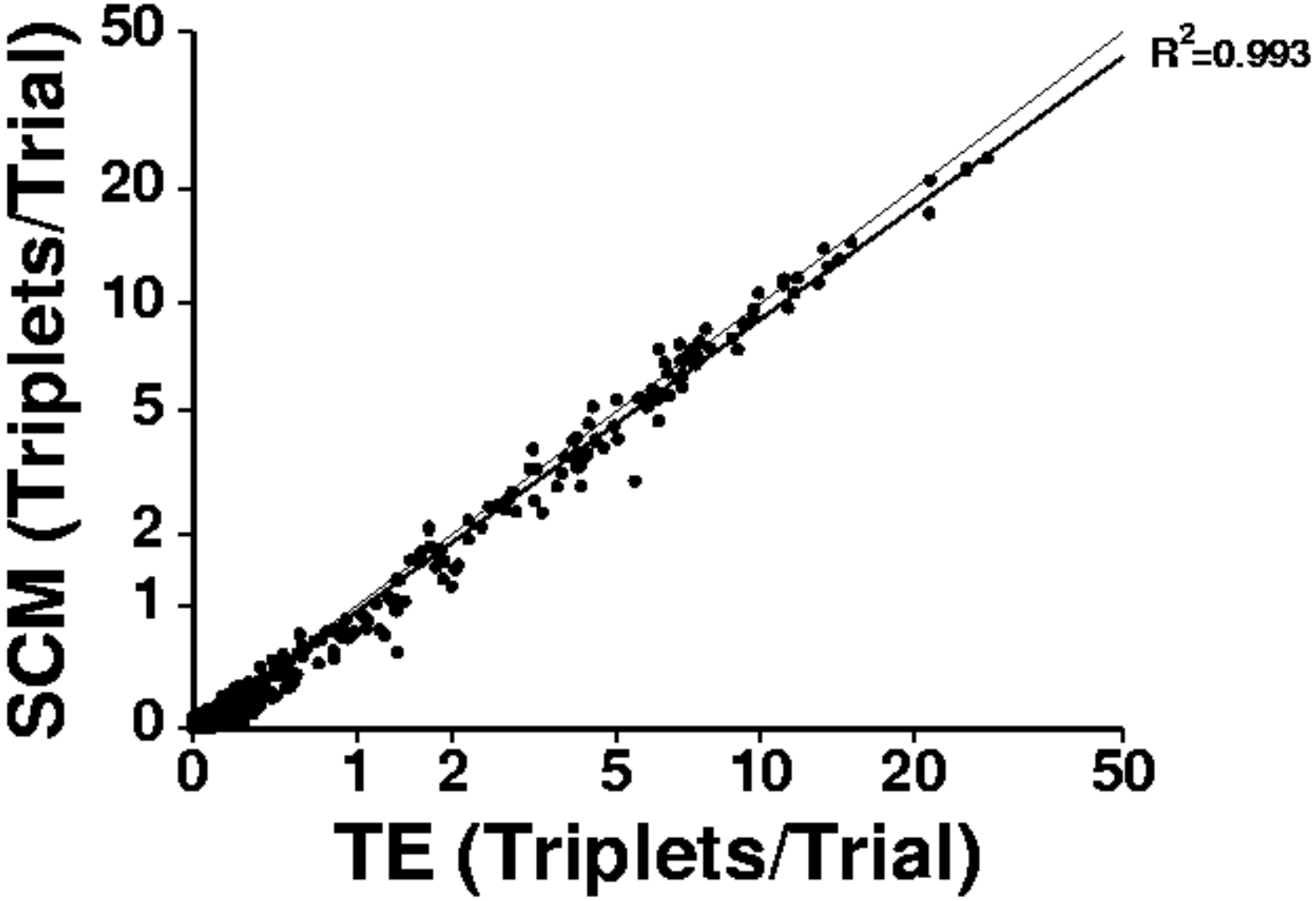
The number of repeating patterns is non-linearly related to spike count. The number of repeating triplets in the TE data showed a non-linear relationship with the number of spikes within the response (Figure 4).



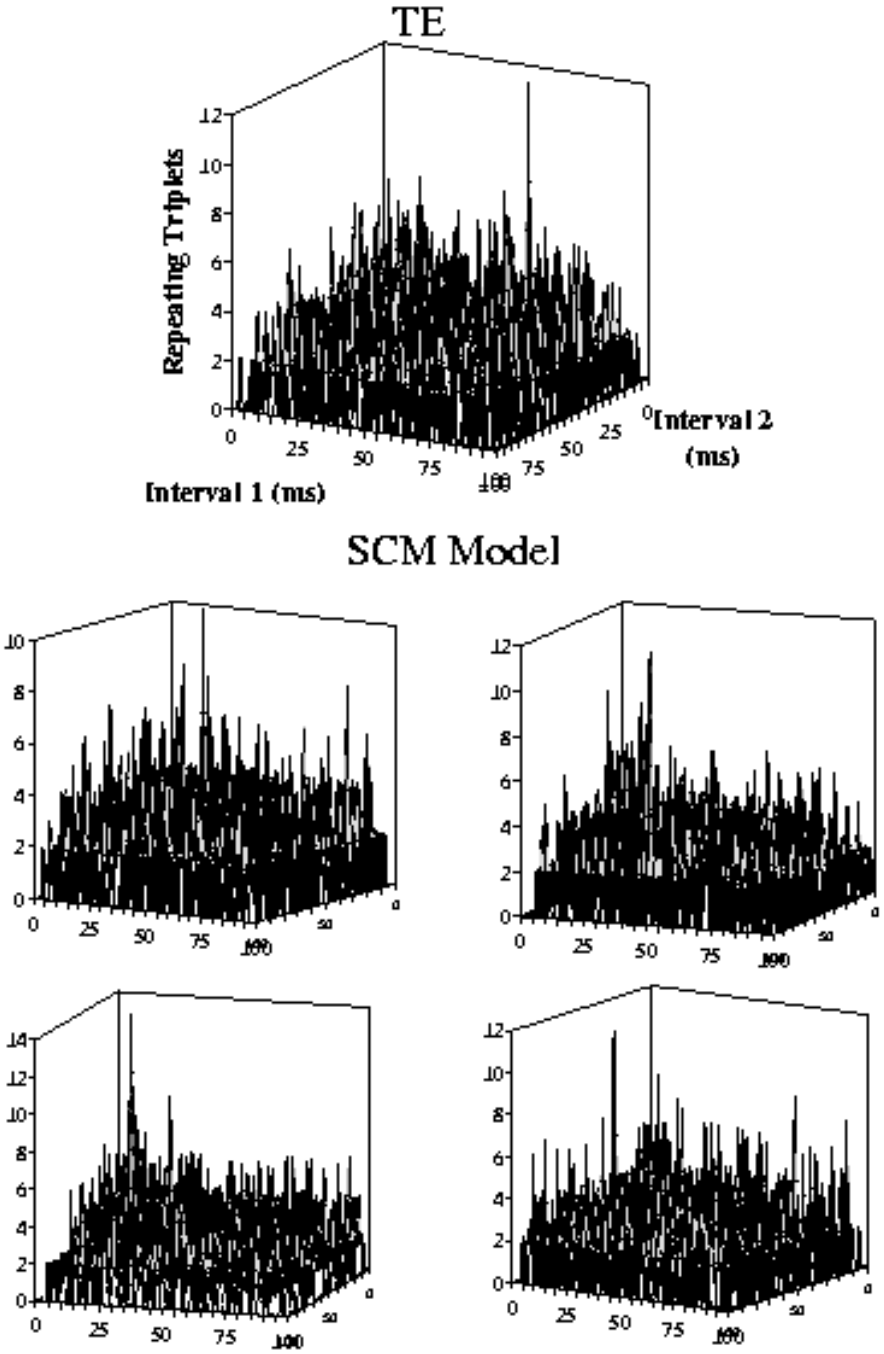
The number of repeating triplets found per trial varied with the different stages of the DMS task. The numbers of precisely timed repeating triplets were higher when stimuli that elicited large responses were presented as non-matches than when they were presented as samples. The highest numbers of repeating triplets were found in the responses to those stimuli that elicited large responses when presented as a match (Figure 5). The increased response variance of the non-match stimuli (Figure 3), combined with the non-linear relationship between spike count and numbers of repeating triplets (Figure 4), explains why, despite the lower mean (Figure 3), the number of repeating triplets observed in the responses to non-match stimuli is higher than the numbers observed in the responses to sample stimuli (Figure 5).



The information from the number of repeating triplets was redundant with the information available from spike count. The information available from spike count was substantially greater than the information available from the number of repeating triplets. Furthermore, the dual code of spike count and number of repeating triplets carried no more information than that carried by the spike counts alone (Figure 6 upper). This was true for all 20 cells (Figure 6 lower).



The SCM model accurately predicts the numbers of precisely timed spike patterns in TE responses. The mean number of repeating triplet found per trial for each stimulus during each phase of the DMS task is plotted against the number predicted from the SCM model in Figure 7. For comparison, the R^2 value obtained from a model based on the non-homogenous Poisson process was only 0.682. Thus the SCM model provides a substantially better fit to the observed data than models based on the NHPP process.



Individual types of repeating triplets are predictable using the SCM model. The observed number of each repeating triplet type was, in general, within the 95% limit calculated from the SCM model. Given the number of comparisons (10,000 triplet types for each of 8 stimuli under the 3 phases of the DMS task for each cell = 4,800,000 comparisons) it is not surprising that there were some cases (~5%) where an apparent excess of particular repeating triplets were observed in the TE data. The upper section of Figure 8 shows an example of the repeating triplet types from the data of one TE neuron. The lower sections show the analysis from the simulated data using the SCM model.

Conclusions

- The numbers and types of precisely timed spike patterns observed in single TE neural responses vary with the behavioral relevance of the visual stimulus.
- The precisely timed spike patterns carry only information that is also available from the spike count.
- The numbers and types of the observed precisely timed spike patterns, including the variation with behavioral relevance, are predicted by the SCM model. Had we used models based on the non-homogenous Poisson process, we would have concluded that the data contained precisely timed patterns that were not consistent with a stochastic process.
- We conclude that the precisely timed spike patterns examined are a consequence of the coarse temporal statistics of the neural responses. Therefore the observed changes in the numbers and types of precisely timed spike patterns in TE neural responses with the behavioral relevance of the stimulus do not support a unique role for these spike patterns in neural processing.