

Deterministic and stochastic aspects of neural codes.
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The brain takes sensory information, processes it to build a model of the environment, compares it to relevant memories, and finally produces organized behavior. At the neuronal level, a central goal for neurophysiology has been to learn what messages are carried in neuronal responses, and thus be in a position to interpret them. At a larger level, it is obvious that there are difficulties, because we are not so much interested the responses of one neuron, but the coordinated response of interacting neurons, a level of analysis that, though now very promising, still largely escapes us, and will play only a small role in this presentation (although it has been a prominent part of others in this course). For much of the discussion below, data will taken from the visual system, the sensory system that by far has received the most attention.

The responses of visual system neurons have been studied ever since Adrian made the first recordings from single neurons. It was obvious from those first recordings that placing a light or visual stimulus on what later became the receptive field (Adrian and Matthews, 1928; Hartline, 1938) would lead to an increase (or decrease) in spiking activity from the single neurons, and before the time of high speed acquisition of data, and high speed data analysis, the responses were characterized by changes the baseline rate. This was first studied by listening to pulses on a speaker, and then later seen in single traces as they went past on an oscilloscope. It was only with the advent of relatively high speed computing that it became possible to examine how the responses changed relatively rapidly with time. Since spike trains are intrinsically time series, it was common in papers before the computing era to speculate about what might be found if neuronal responses, i.e., the spike trains, could be examined more closely. The central theme of this discussion will be what is noise and what is signal?

The nature of the experiment we carry out affects the types of responses and the phenomena we observe. If we present rapidly changing stimuli, that is, if we repeatedly hit the system hard, we observe one set of phenomena, that is responses that seem to have spikes tightly time-locked to some temporal feature of the stimulus time series, and if we present stimuli either by having them change more slowly, or present them as a step in time, the system has time to 'ring' or settle, there are other features, that is responses seem considerably more variable across a set of presentations of the same stimulus. Below the emphasis will be on the situation in which a stimulus 'steps' on and stays on for a period of 300-400 ms, but reference will be made to the situation in which stimuli are changed rapidly, for comparison. As yet these two sets of phenomena have not been completely connected, but each reveals import features of the visual system, and perhaps neural processing on a larger scale.

The first consideration is what representation of the response is needed to characterize the responses. The classic measure has been the response intensity, estimated from the spike count over some time period, of the response. For now we will forgo the issue of how long to count spikes; we will count them for the stimulus duration (delayed by a short

period to account for most of the latency), which then leads to the question of for how should the stimulus be presented? Consider the situation of a person (or a monkey) sitting in a chair looking around. Such an individual might be looking at something, perhaps a spot of light. We then imagine the monkey making a rapid or saccadic eye movement toward a new object of interest. At the end of the eye movement a new visual stimulus will have appeared on the receptive field of the neuron, and the neuron should respond when the stimulus falls onto the receptive field.

Even though humans and monkeys can learn to fixate without much in the way of eye movements for much longer periods, saccadic eye movements generally occur every 300-500 milliseconds in 'normal' situations, making this 300-500 ms period seem to be an appropriate interval over which to examine neuronal responses of neurons in the visual system. The situation during each fixation between saccadic eye movements is often mimicked in the laboratory when recording single neurons by having the monkey fixate a little spot of light, with stimuli being presented every 300-500 milliseconds on the receptive fields of the neurons (Figure 1). Under this scenario, the sensitivity of the neuron can be quantified with the spike count, which for oriented bars in primary visual cortex, V1, will give rise to a classic orientation tuning curve, although the responses appear to vary considerably from presentation of a stimulus to another (Figure 2). Given that the response occurs over time, it is natural to examine the time course of neuronal responses after a stimulus appears on the receptive field of a neuron. In the example shown in Figure 3, it is clear that the firing rate over time is related to the stimulus, even though in this example the total number of spikes and the variances of these two responses are the same when counted during the whole period of stimulus presentation (here 320 ms). And again the variability in both the number and timing of spikes is prominent. However, it is also clear that the envelope of the firing rate (the low-pass filtered version of the spikes) is different across the two stimuli. Thus, even though these two sets of responses have the same number of spikes over the whole counting interval, the time course of when the spikes occur appears reliably different.

How useful is this difference in the time course of the responses? A valuable approach to this problem has been to ask how much extra information the receiver of the response can obtain by being sensitive to the time course of the response. This requires developing an approach to quantifying this information. At this point in this course I assume that you are all familiar with information theoretic measurements. For the purposes here, the basic definition of mutual information is required, i.e., the mutual or transmitted information, $H(r,s)$, is the difference between the entropy of the spike train (or stimulus), $H(r)$, and the entropy of the response when a stimulus is presented, $H(r|s)$. The r and s can be interchanged because in this form mutual information is symmetrical with regard to the sender and receiver of a message, even if the physical channel might not be.

For now, consider increasing the complexity of the response beyond the simple spike count taken from the entire stimulus presentation period. In Figure 3, it seems clear that it might be good to low-pass filter the response. One approach to determining the precision needed is to low-pass filter the response, i.e., smooth it, with different degrees of smoothing (Heller et al., 1995; Victor and Purpura, 1996). It has also been useful to determine decompose the responses and progressively add components to the

representation to allow the responses to become more ‘complex’, or have more temporal modulation, i.e., to have more wiggles over time.

The decomposition can be done in any number of ways. One straightforward way to do this is to take the principal components of the set of responses and decompose the responses using them. The principal components are the eigenvectors of the data domain covariance matrix, and form an orthogonal set of, in this case, temporal waveforms derived from the data themselves. These can be used to represent the responses. The responses in Figure 3 are decomposed into their first few principal components in Figure 4, where it can be seen that the value of the first principal component is nearly identical, as it should be because the first principal component is (nearly) always closely related to the number of spikes. However, the second principal components coefficients are very different, here having opposite signs. This is because the second principal component has a shape that readily represents the dip of lack of it seen in these two responses. Using more (higher) principal components adds little, if any, additional information in this example. For the cases where the principal components have been used to distinguish responses, the number of them that carry independent information over the preceding ones, has been small, between 2 and 5, generally (a lot of us). In this case the value of measuring the information is that the responses can be considered a vector, with the length of the vector being increased from one to several principal components (specifically the code uses the coefficients of the principal components). For this type of analysis increasing the number of principal components beyond two or three does not generally increase the amount of information (Optican and Richmond, 1987; Richmond et al., 1987; Richmond and Optican, 1990; Richmond et al., 1990; Gawne et al., 1991; McClurkin et al., 1991a; McClurkin et al., 1991b; Kjaer et al., 1994)

The need for this small number of principal components also suggests that the spikes do not generally need a large number of degrees of freedom to represent them, that is, blurring them out in time does not hurt the potential decodability of the responses. Several measurements have estimated that the precision of the spike timing is on the order of 10-20 ms, or longer in these experiments using stimuli flashed onto the receptive fields (Heller et al., 1995; Victor and Purpura, 1996, 1998).

One question that has come up is whether different parts of the neuronal responses can be identified with different stimulus characteristics. There are two types of response structures that have been given such an identification, and this identification has only really been done in V1. These structures are single vs doublet spikes, i.e., whether spikes tend to be grouped into pairs or whether they occur singly, where it has been shown that, for complex cells, the amount of clustering is related (tuned) for spatial frequency, and the single spikes are tuned for contrast (Cattaneo et al., 1981; DeBusk et al., 1997). It has also been shown for complex cells that the response strength is closely tuned for orientation across a wide range of contrasts, whereas the latency changes with contrast without a big effect on response strength (DeBusk et al., 1997).

The information is limited by the variability of the responses. If every stimulus presentation elicited exactly the same number and pattern of spikes, the information would be directly computable by counting the number of unique responses. The source of

this variability is not really known, and under conditions of rapid changes in the stimulus responses can highly reproducible so the variability can be very low. It has been speculated that the variability seen during these 300 ms or longer stimulus presentation arises from little differences in eye position or eye movements. This, however, has not been easy to settle. Many studies have examined the variability of the responses in some detail, have shown that the variability is proportional to the firing rate (although not equal to it as would be the case for a pure Poisson process)(Dean, 1981; Dean and Tolhurst, 1983; Gershon et al., 1998; Wiener and Richmond, 1998, 1999). If the variability were due to the small eye movements then in experiments with paralyzed anaesthetized animals the variability should be smaller, which it is not (Dean, 1981; Victor and Purpura, 1996). Thus, the source of the variability is still not really known.

Another alternative is that the variability arises from encoding sources within the nervous system that do not covary with the stimulus, e.g. arousal or focal attention, and these therefore appear as unaccounted for variability, but are not true noise. At a minimum, the variability will have to be described and its influence on the organization of neuronal responses must be taken in account. The variability is seen both in the number and timing of spikes, and although it was for a long time not completely appreciated, it is now clear that the variability in the number of spikes influences our estimates of relating the number of spikes to their timing. This latter point will be theme for what follows.

The firing rate and the variability are generally linearly related on log-log coordinates. The slope and intercept of the linear regression line connecting them are not one and zero, in general, showing that they do not arise from a simple Poisson process. There has been and continues to be a lot of discussion of this slope, and the slope can have a big influence on how information is coded. In the early visual system, the slope in many experiments has been seen to be larger than one, which, since the plots are on log-log coordinates means that the variability rises exponentially with the mean. If one takes the mean-variance relation seriously, and there is work to suggest that might be reasonable in many instances, this relation describes how the variance is related to the mean, and one can calculate the channel capacity, i.e., the maximum information that can be sent through channel. In principle, it is necessary to try every stimulus that could ever be put into the channel. However, if one realizes that every stimulus yields a spike count and the variance is directly related the mean, one can estimate what distribution of spike counts would be needed to maximize the mutual information between the stimulus (here ghosted by the average spike count) and the individual noisy responses (Wiener and Richmond, 1999).

A further identification can be made. We know that the mean response is linearly related to the variance. What about the temporal variation, for example the second principal component? If we plot the coefficients of the variance of the second principal component against its mean for each stimulus, there is only a weak linear relation. However, the variance of the second principal component is related to the spike count (Figure 6) (Wiener and Richmond, 1999). This can be understood in stochastic terms. Consider stochastic sampling of a uniform point process. If the spikes are placed stochastically, the number of combinations of spikes that arise by chance is $\frac{n!}{k!(n-k)!}$, or, n choose k ,

where n is the number of bins for the time period (usually taken to be 1 millisecond, and k is the number of spikes to be placed in the bins. If the number of spikes changes, the number of patterns that occur by chance necessarily change also; n , the number of bins, is constant, and, k , the number of spikes, changes stochastically across stimulus presentations. For example 200 choose 2 yields 19,900 combinations of spikes by chance, and 200 choose 3 yields 1,313,400 combinations. Since a small change in spike count can dramatically change the number of spike patterns expected by chance, any effort to describe what happens must first and carefully account for the variability in spike count. This then leads to a line of work to evaluate the impact of this necessary relation between spike count and numbers of spike patterns.

Finally, there is one more indication of this relation between the number of spikes and the number of spike patterns. If the coefficients of the first and second principal components from one neuron are placed on a scatter plot, they fill a cone, with the apex at the lowest spike count. This shows that the number of response types grows with the spike count (and would continue to grow until half the bins could be filled). Thus, when there are only a few spikes, there are only a relatively few spike patterns available for coding.

It is certain that there must be coordination of activity among large ensembles of neurons, but it is not yet known how information is handled in ensembles. An intriguing hypothesis about cortical processing is that there are patterns of spikes hidden within the apparently noisy responses of the sort above. This hypothesis arises from strong theoretical considerations arising from straightforward, elegant considerations about cortical connectivity and neuronal biophysical properties (Abeles, 1991). The conclusion of these arguments is that there might be in dynamically changing neuronal ensembles patterns of spikes within and across neurons that are strongly related to cognitive events. These patterns are difficult to identify in experimental data because the organization of ensembles is continually changing due to the dynamics of the neurons and their connections. One possible method to identify these spike patterns is to enumerate the patterns (a painstaking process) and identify those that seem too frequent (or too sparse) given the hypothesis that they arise by chance. That is, the null hypothesis is that these patterns arise by chance.

As an example we examine what happens when repeating triplets (sets of 3 spikes separated by a set of 2 intervals that repeat within a single trial) are identified and counted in the lateral geniculate nucleus (Figure 7). The spikes participating in repeating triplets are identified in red. The number of these can be counted and used to extend the spike count code. When that is done, there is stimulus related information available from the number of repeating triplets. However, when the number of repeating triplets is used to extend the spike count code, there is no extra information over that carried by the spike count alone (Figure 8). This suggests that the triplets are related to the spike count. It is possible that the triplets are related to some other process. One approach to this issue is to develop a direct connection between the spike count and the number of triplets (Oram et al., 1999). The way this has been done was to develop a model in which the number of spikes matched those that found in a recording experiment, and to generate the exact times of spikes stochastically. When this is done for data in the LGN and V1, the number

of repeating triplets in the experimental data is found to be exactly what is predicted from the computational model. When the model is checked for the number of particular triplet sets, it was found that the numbers of repeating triplets of specific types followed exactly the distribution found in the data. When the model was run assuming that the spike counts came from a single homogeneous Poisson process, the numbers of triplets did not match. Thus, there are two issues that must be checked. The first is whether the spikes came from a Poisson process (no), and whether they are consistent with a stochastic process (yes).

This model uses the spike count distribution, the peristimulus time histogram (or the spike density), and the cumulative spike density (Figure 9). These features are the same features that are needed in order statistics, a branch of statistics that describes the probability distribution of the k^{th} event of n expected events, that is the probability distribution for elements stochastically chosen from a known probability distribution. We can think of these events the 1st, 2nd, ...etc spikes, and the order statistic describes where these spikes are likely to fall in time when drawn in order using the PSTH.

The observations lead to the strong hypothesis that spikes are stochastically related to the underlying time dependent rate function. At the other end of the spectrum is the proposal that some, if not all, spikes are placed according to some deterministic rule. An intermediate proposal is that at least some spike patterns are deterministic. To study this issue requires a proposal of how to recognize the spike patterns. One heavily studied version of this has been synfire chains. Specifically it has been suggested that exactly timed patterns in spike trains arise as a signature of synfire chains, which themselves are a type of self-organization of dynamically changing ensembles (Vaadia et al., 1995; Seidemann et al., 1996). The null hypothesis that was first studied was that responses arise from a time-varying or non-homogeneous Poisson process. It is quite easy to find that the number of specific triplets, for example, is not consistent with this hypothesis. However, there are two parts of the hypothesis. The first is that the times of spikes are stochastically determined. The second is that the process is non-homogeneous Poisson. However, it is easy to show that the few responses are consistent with non-homogeneous Poisson. The variance should equal the mean, which as can be seen above where the mean-variance line is above the identity line, the mean-variance line is above the identity line. Also, 2/3 of the spike count distributions are not fit well by single Poisson distributions.

If the spikes are placed stochastically, the number of combinations of spikes that arise by chance is $\frac{n!}{k!(n-k)!}$, or, n choose k , where n is the number of bins for the time period (usually taken to be 1 millisecond, and k is the number of spikes to be placed in the bins.

It has now been shown that if the spike count distribution is matched (Figures 9 & 10), and then the stochastic model is used, the types of triplets are almost exactly predicted (Figure 11). This type of model can be implemented via a simulation method. However, given the success of the match between simulation, it can be recognized that the method of simulation suggests that order statistics can be usefully applied to understanding this

problem. Order statistics give the unconditional probability distributions for the k^{th} event out of n events. For example, we can calculate the probability distribution for the 3rd event or spike out 10. Order statistics explicitly needs the counts, the density of events (PSTH), and the cumulative distribution, all of which we can estimate from data (Figure 12).

However, we do not just want this unconditional distribution. Rather if the conditional distribution is available, a decoder or an accurate simulator can be constructed (Wiener and Richmond, 2003).

First we develop this.

$$h(s, t) = \binom{n}{k} k F^{k-1}(t) f(t) [1 - F^{n-k}(t)]$$

$h(s, t)$ the probability of the spike k at time t . n choose k times $(k-1)$ is a normalizing factor, $F(t)$ is the cumulative distribution from $f(t)$, the rate function over time (estimated as the spike density or peristimulus time histogram). We would like the conditional estimate based on the time or spikes that have already gone by. We do this by working recursively. We simplify this to be the probability of the first spike, $h(s_1, t)$.

We will consider each spike the next first spike. We need one more step. We are interested in the probability of the stimulus, regardless of the spike count. Therefore we weight the orders statistics of the different spike counts by the probability of that spike count occurring and sum these. If we do that, we can then estimate the probability of a stimulus, s , at time t , through Bayes theorem (Figure 13). From this we can estimate the probability of the stimulus, $p(s, t)$, at time t . If we then take these new probabilities as the new $p(s|t)$ for $p(s)$, we can iterate through the spike train. Thus, by stepping through the spike train updating $p(s)$, we are estimating the probabilities of the different stimuli. If we apply some decision, maximum liklihood for example, we can make a guess as to what stimulus is eliciting the spike train.

This approach is general, requiring two assumptions. The first is that the spikes are stochastic, and the second is that the spike density is the estimate of the rate function, that is, the density of expected spikes over time.

To carry out the decoding as described above, the spike density, cumulative spike density, and spike count distribution will have to be recalculated starting at every spike. This is general, and therefore must work. However, It is time-consuming, and it would be better to have some model of the responses that makes these calculations easier. To this end one can examine the spike count distribution to determine whether some straightforward model of it would help. One that has helped is to model the spike count distribution as a sum of Poisson distributions (Figures 14 & 15). Then the order statistics can be calculated from this model. This model is the same as saying that, given the spike density, the rate for the nonhomogeneous Poisson process on any given trial is selected stochastically from one of the rates of the fit Poisson processes. This fitting of the spike count distributions by a few (almost all needed 3 or fewer) Poisson distributions is an adequate representation of over 95% of the spike count distributions examined in V1 [ref]. With these identifications, decoding can proceed millisecond-by-millisecond, whether there is a spike or not (Figures 16 & 17).

Figure legends:

Figure 1: Orientation tuning for a V1 complex cell. The polar plot shows the orientation tuning curve for stationary oriented bars, with distance from the center indicating response strength, and angle indicating bar orientation.

Figure 2: Orientation tuning for oriented bars, with the heavy line connecting the mean responses. The error bars show standard error of the mean. The dots are the spike counts for all of the individual trials. Any orientation has a substantial probability of eliciting a response with 10 spikes. This gives some intuition about the decoding problem for this type of response.

Figure 3: Responses of a V1 complex cell to two different black and white patterns. The total number of spikes and the variances over the whole interval are equal. However, the rasters and spike density have different time courses, making it seem desirable to utilize the temporal pattern of the response (the different shape rate functions) to decode the responses. Note that the dip in the right hand response is about 30 milliseconds wide, making it seem entirely plausible to believe that this is detectable by a target neuron.

Figure 4: Principal decomposition of the two responses shown in Figure 3. The principal components were derived from the covariance matrix calculated from all of the responses to all of the patterns. The average spike densities are shown at the top. The middle shows the weightings of the first 5 principal components. The bottom shows the shapes of the principal components (the eigenvectors of the covariance matrix) themselves, as modulations over time. The time-dependent mean was subtracted from each response before the covariance matrix is built.

Figure 5: Scatter plot of means vs variances for 272 black and white images presented on the receptive field of a V1 complex neuron. The solid line is the regression line, and the dotted line is the identity line where the points would lie if the responses arose from a Poisson process.

Figure 6. The scatter plot for the variance of second principal component values against the mean of the second principal component on the left, and against the spike counts on the right for each pattern.

Figure 7. The red spikes show one repeating triplet. Note that other spikes can intervene.

Figure 8. The information about the stimuli for a spike count code, a number of repeating triplet code, and for the joint code. The joint code carries no more information than the spike count code, suggesting that the triplet code is redundant with, but less reliable than, the triplet code.

Figure 9. A spike density, the cumulative spike density, and mapping 6 (presumably) random numbers (vertical axis) drawn from a uniform distribution through the cumulative distribution to give a simulated spike train that is related to the original spike density.

Figure 10. The spike count matched model for matching spike counts with a desired (here experimentally obtained) distribution.

Figure 11: The match between the spike count matched model predictions and data taken from LGN and V1.

Figure 12: The three elements that go into the spike count matched model and will be used by the order statistics model.

Figure 13: The equations for counted weighted order statistics. h is the order statistic for the first spike with count n and stimulus s on the right, and stimulus s across all counts on the right. $p(n)$ is the probability that a particular spike count will occur for stimulus s . Bayes theorem for iterating through the spike train. Each new $p(s|t)$ on the right would become $p(s)$ in the right for the next step. Thus, $p(s)$ incorporates the memory of the decoding up to the current time.

Figure 14. Fitting the spike count histograms for 3 different stimuli. They are fit by 1, 2, and 3 Poisson distributions. The relative weights will be denoted by λ in the subsequent figures.

Figure 15. The mixture of Poissons model to simplify calculating the order statistics.

Figure 16. The probability transformations used in the order statistics model for the two responses shown in Figure 3.

Figure 17. Decoding the spike train at the top for the two responses shown in Figure 3. The spike densities are shown again at the bottom. Note that the decoding guess can change and decrease at times. This decoding turns out to be done by the latency difference for the most part.

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Figure 1.

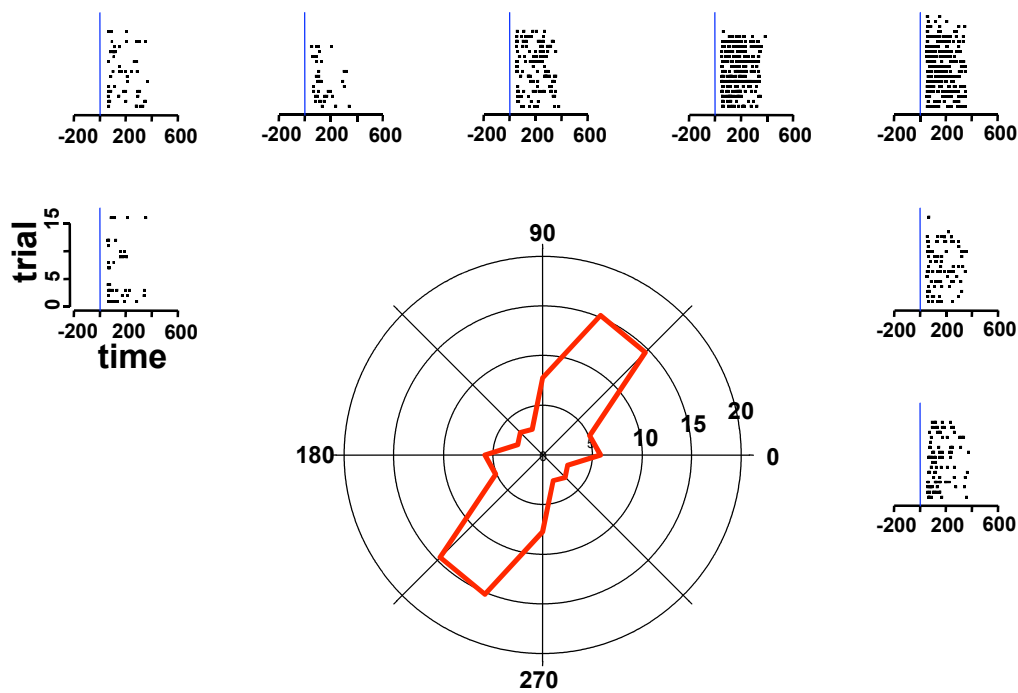


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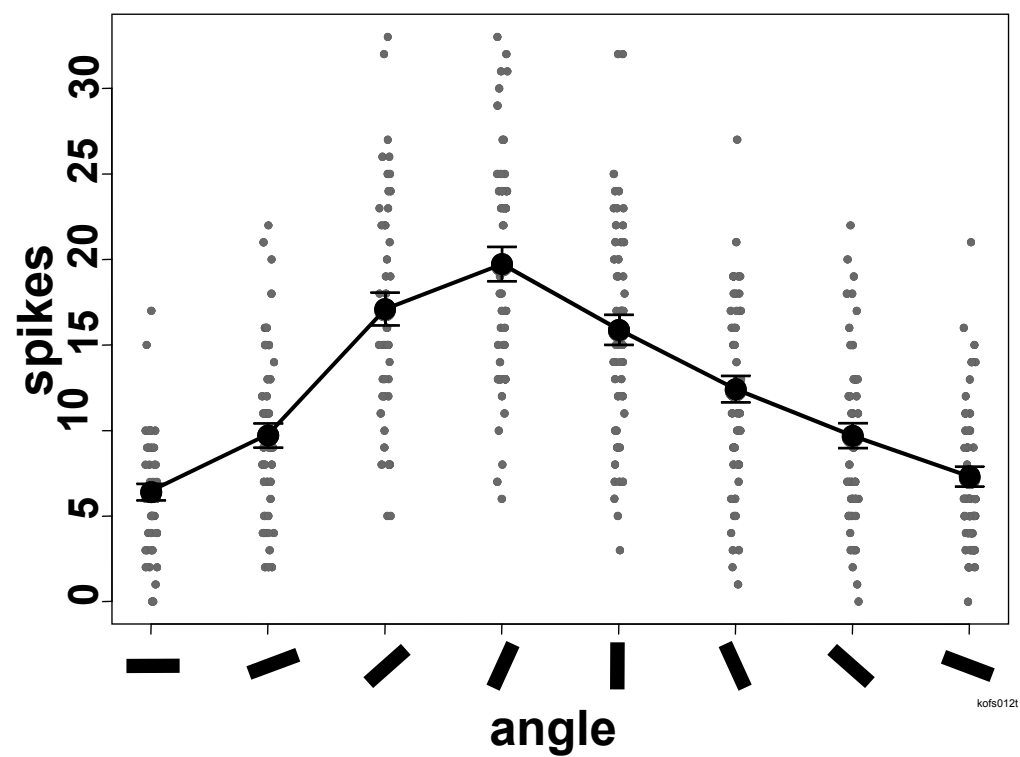


Figure 3:

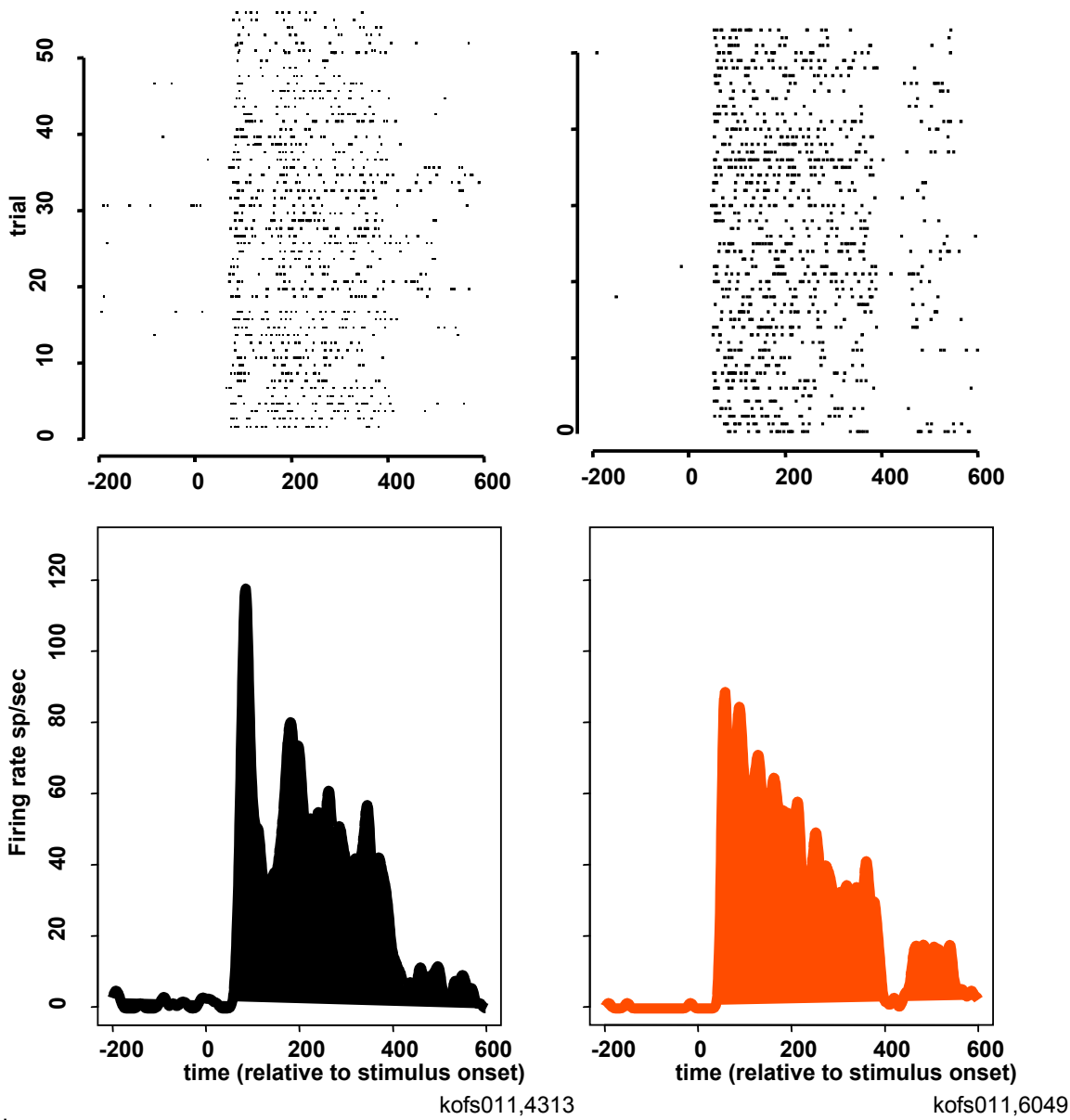


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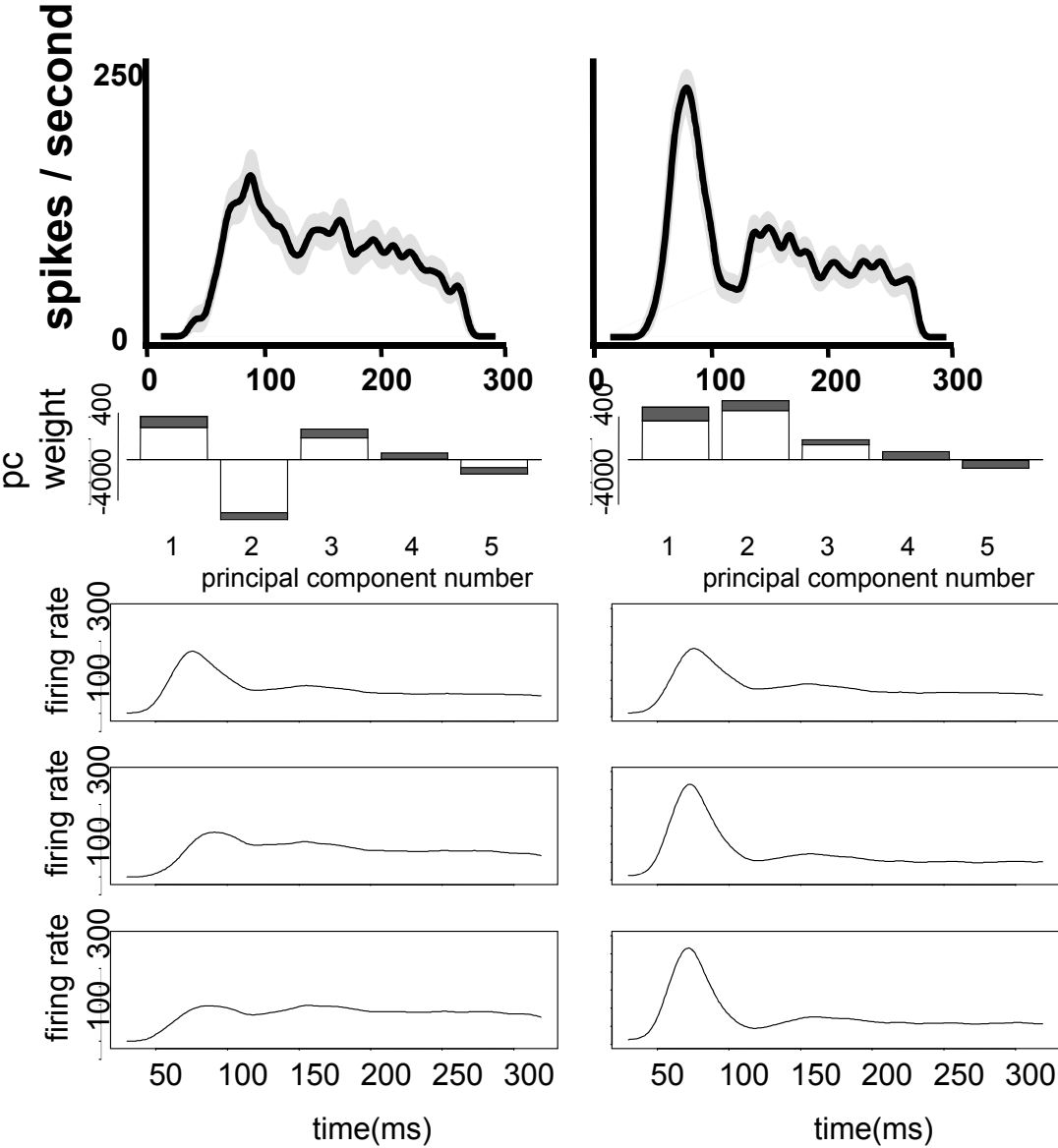


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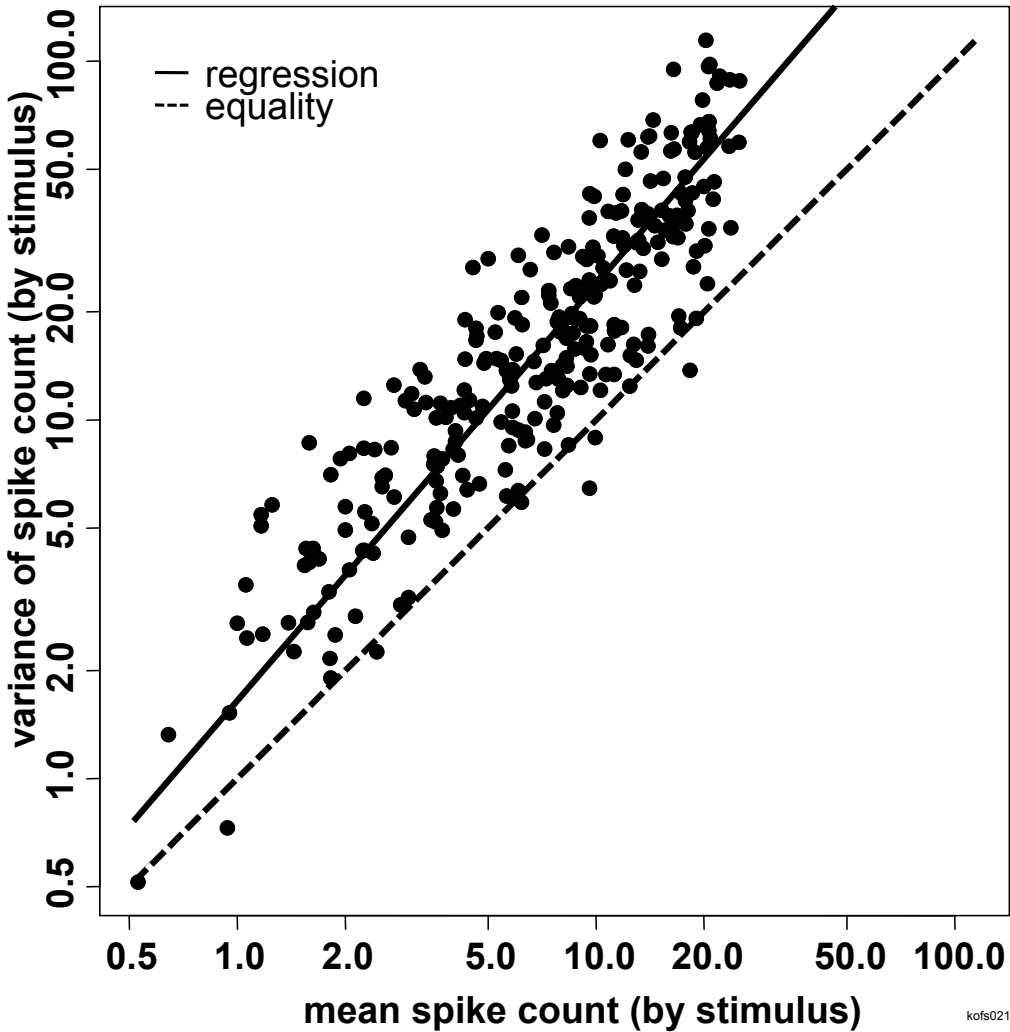


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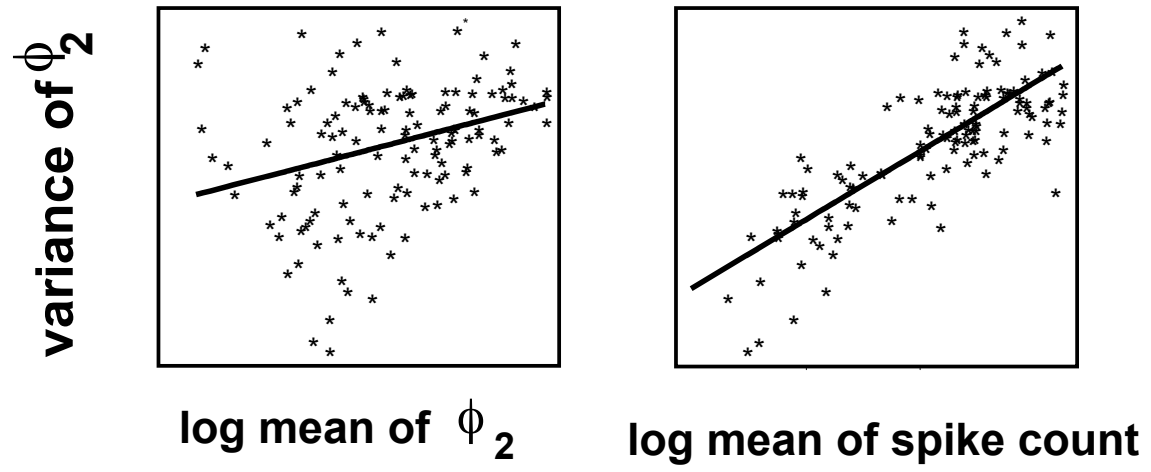
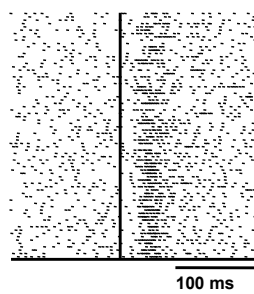


Figure 7:

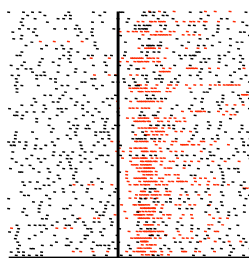
REPEATING TRIPLET IDENTIFICATION



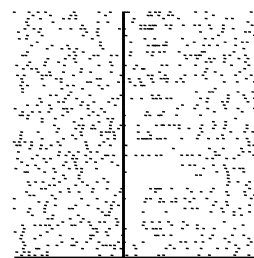
Spikes participating in triplets in LGN responses.



ALL SPIKES



**HIGHLIGHTED
SPIKES IN
TRIPLETS**



**SPIKES NOT IN
REPEATING
TRIPLETS**

Figure 8:

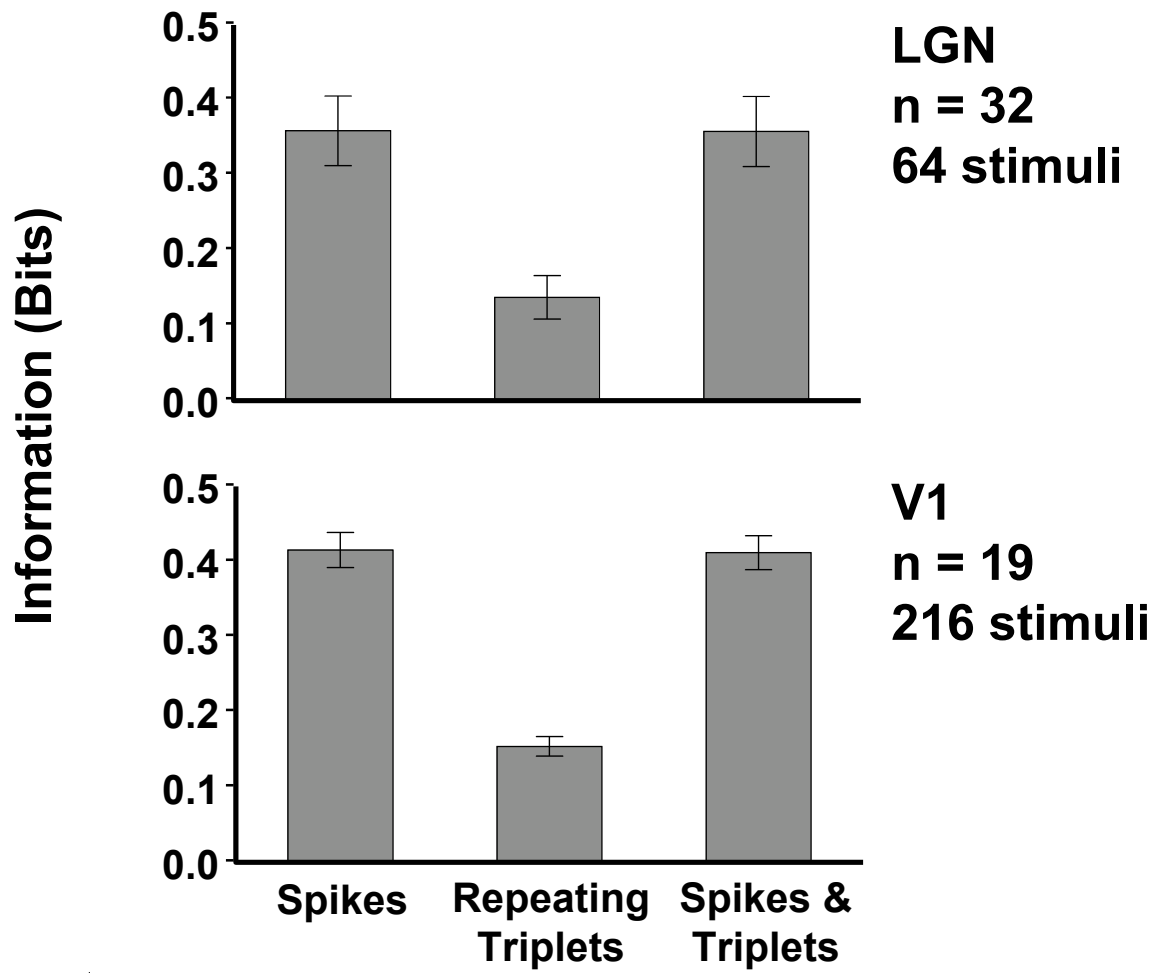
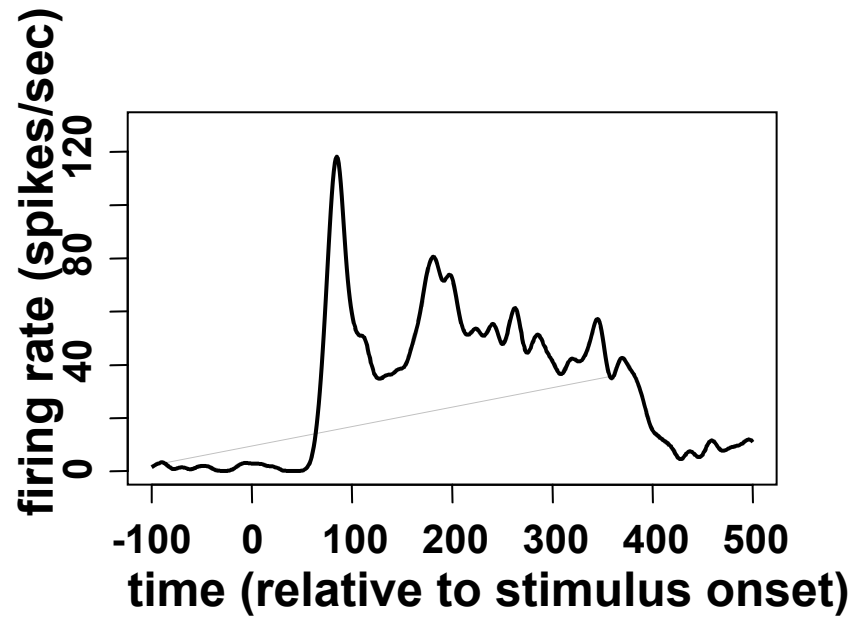
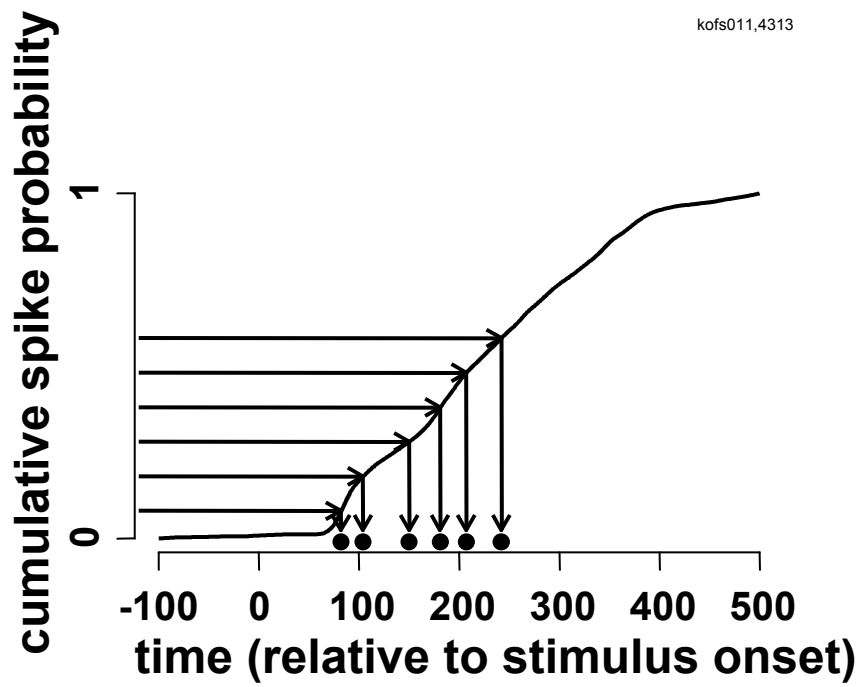


Figure 9:



kofs011,4313



kofs011,4313

Figure 10:

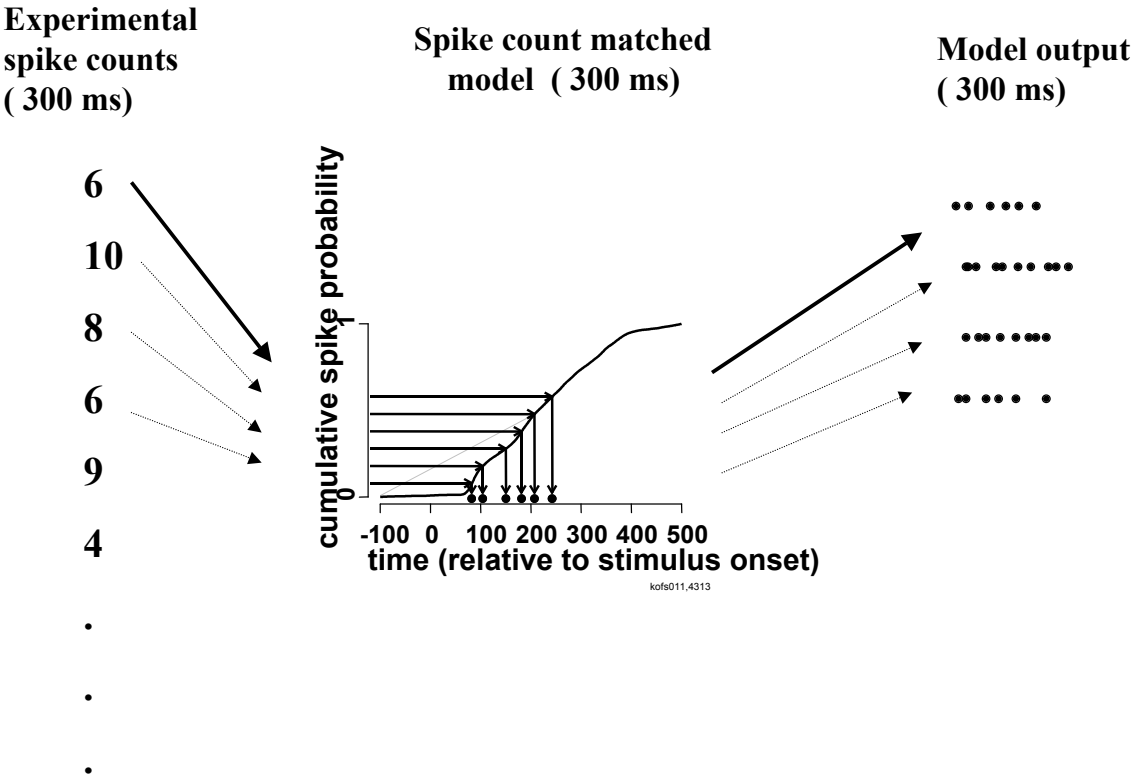


Figure 10:

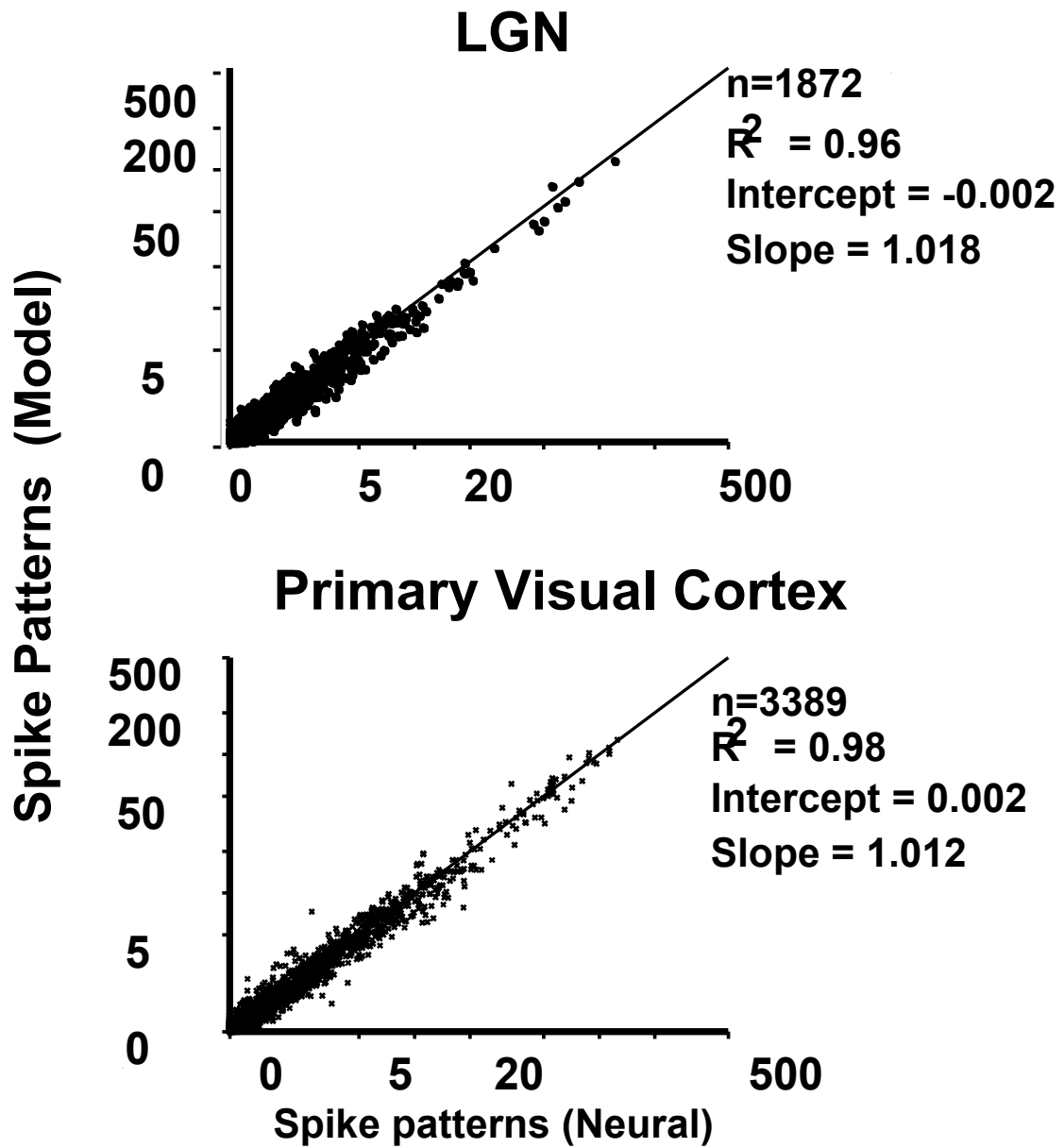


Figure 12:

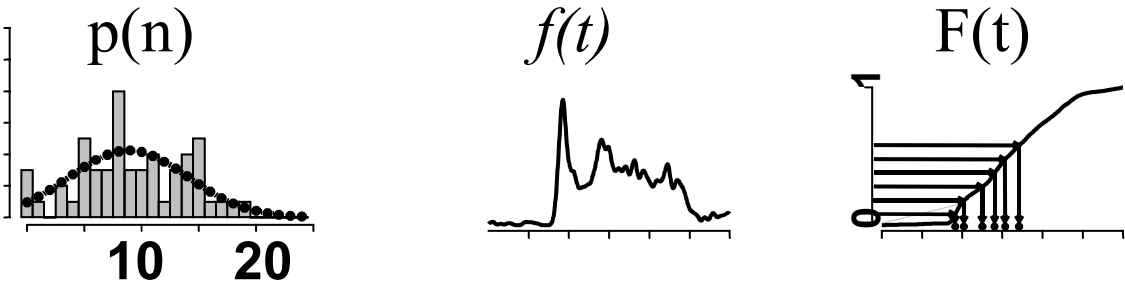


Figure 13:

Count weighted order statistics:

$$h_{1,s}(t) = \sum_n p_s(n) h_{n,1,s}(t)$$

For decoding use Bayes' rule:

$$P(s \mid \text{next spike at time } t) = \frac{p(s) h_{s,1}(t)}{\sum_{s'} p(s') h_{s',1}(t)}$$

Figure 14:

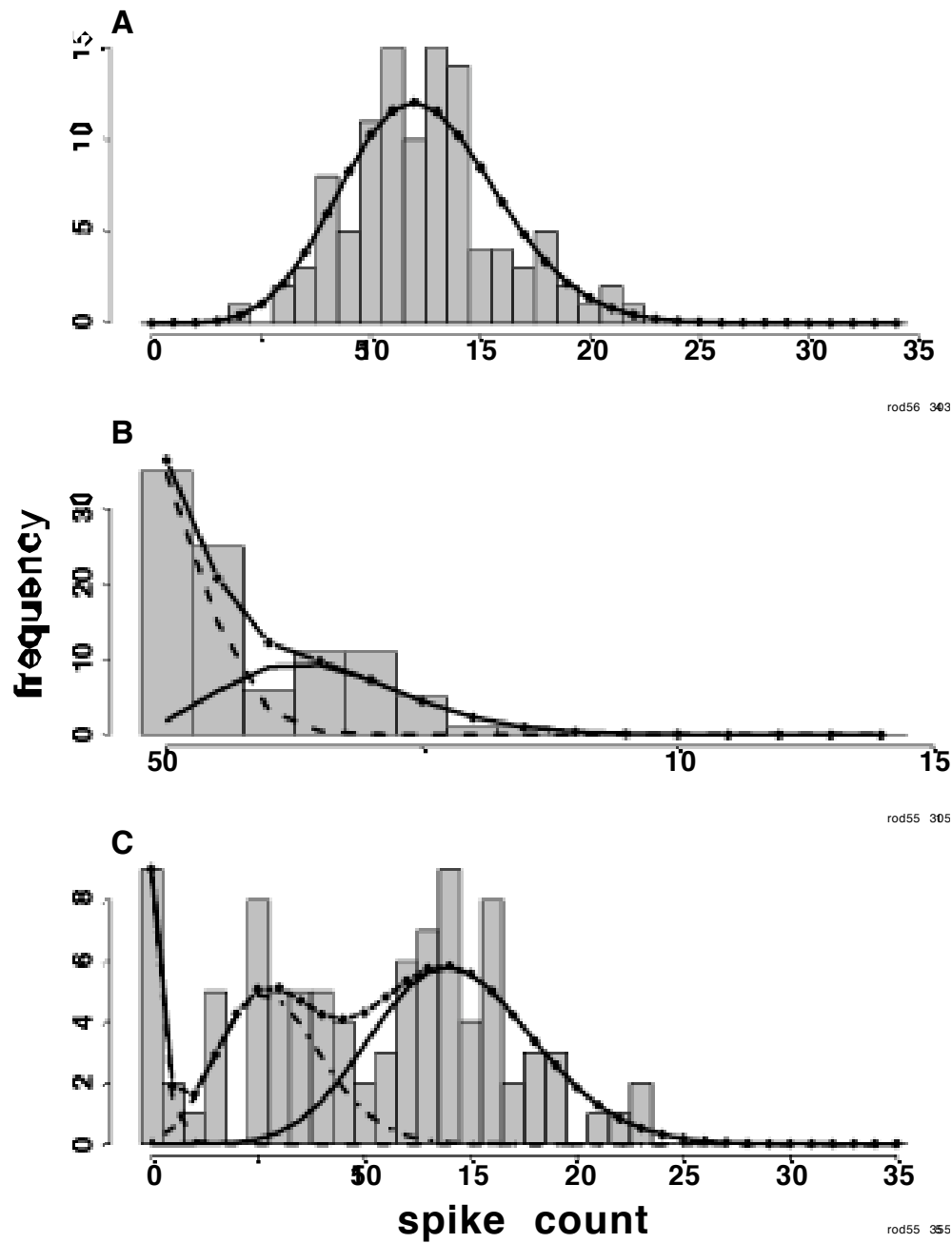


Figure 15:

The probability of spike t , is given by the sum of the mixture of Poisson processes weighted by the proportion of the Poisson distributions used to fit the spike count distribution.

$$P(t_j | s) = \sum p(\lambda_{s,i}) P(t_j | s, \lambda_{s,i})$$

$$P(t_j | s, \lambda_s) = \lambda_s f_s(t_j) e^{-\sum_{t=t_0}^{t_j-1} \lambda_s f_s(t_k)}$$

$$P(t_j | s, \lambda_s) = \left[1 - e^{-\lambda_s f_s(t_j)}\right] f_s(t_j) e^{-\sum_{t=t_0}^{t_j-1} \lambda_s f_s(t_j)}$$

Figure 16:

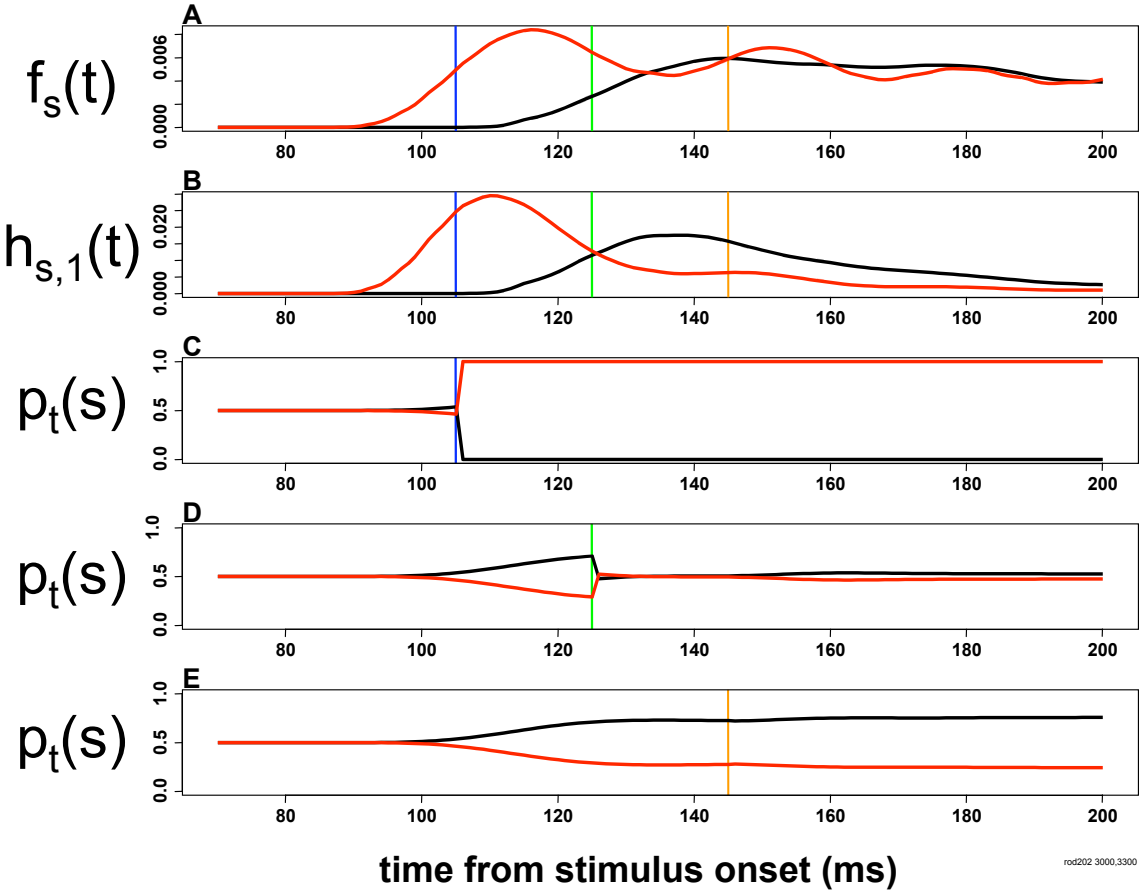


Figure 17:

