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# Joint Peri Stimulus Time Histogram (JPSTH)



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## Definition

The joint peristimulus time histogram (JPSTH) provides the two-dimensional time-resolved correlation of two neurons with respect to a trigger event. A specific correction removes the effect of the trigger on the individual neuronal responses and thus highlights the excess correlation between the two neurons.

# **Detailed Description**

The temporal relation between two spike trains is usually studied using the ordinary crosscorrelation (see entry ▶ "Correlation Analysis of

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Parallel Spike Trains") together with the shift or peristimulus time histogram (PSTH)-based (see entry  $\triangleright$  "Estimation of Neuronal Firing Rate") predictor to partially compensate for firing covariation. These measures are averages over the entire length of data and hence ignore dynamics. This means we can only infer the static average interaction between the neurons. A portion of the dynamics may be associated with the repeated presentation of stimulus, and it is this portion that is delineated by the JPSTH (as an average over the presentations). The JPSTH also gives a better approach to extracting excess correlation than do the traditional shift or PSTH predictors (Aertsen et al. 1989; Palm et al. 1988).

Construction of the JPSTH begins with creation of the scatter diagram shown in Fig. 1. For each presentation of the stimulus, we take the stimulus time as origin and lay off the activity of the two neurons, each along its own axis as indicated. Points are then plotted on the plane at all logical ANDs of the several action potentials on each axis. The process is repeated for subsequent stimuli, building up a scatter of points on the plane. Various features of the neural activity will produce regions of higher point density. If, for example, one neuron responds to the stimulus with a brief increase in firing rate, there will be a bar of high density of points parallel to the appropriate axis at a location corresponding to the response latency. If there is a high probability of near coincidences in the two trains of action potentials, there will be a bar of high density of

Deceased – George L. Gerstein passed away on March 28, 2018. Upon his decease, Ad Aertsen agreed to become a Co-Author, taking care of updating this Chapter.

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points parallel to the principal diagonal and at a distance from it that represents the latency of the favored near coincidences. There may be modulations of density along this bar, indicating the averaged stimulus-locked modulations of the probability for the near coincidences.

The scatter diagram described in the previous paragraph is constructed at the maximum temporal resolution available in the data, that is, corresponding to a single clock tick. In order to allow statistical manipulation of the point densities, we need to make coarser bins. The appropriate types of bins are shown in Fig. 2. For the JPSTH matrix, we use square bins at the same values that are used for the ordinary PST histograms of each spike train (Fig. 2a). For the region near the principal diagonal, we use the bins indicated in Fig. 2b, producing the PST coincidence



Joint Peri Stimulus Time Histogram (JPSTH), Fig. 1 Construction of JPSTH

histogram. This measures the averaged stimuluslocked near coincidence probability in the same sense as the ordinary PST histogram measures the averaged stimulus-locked firing probability of each neuron individually (see entry ▶ "Estimation of Neuronal Firing Rate"). Finally, by summing along the para-diagonal bins shown in Fig. 2c, we produce the ordinary cross-correlogram of the two spike trains (see entry ▶ "Correlation Analysis of Parallel Spike Trains"). Note that since these bins are not of equal length (and hence area), we must either normalize by the bin length or compute a larger matrix so as to allow making all bins of equal length.

We now apply the JPSTH measurement to a set of spike trains produced by a simulator. The simulated circuit arrangement is shown in Fig. 3. The observed neurons "10" and "12" are each "spontaneously" active because of independent and stationary inputs from networks G10 and G12. In addition, a periodic stimulus input briefly elevates firing probabilities for the observed neurons. Finally, there is an excitatory synaptic connection from neuron "10" to neuron "12" whose strength is itself modulated by the stimulus; this is indicated in Fig. 3 by the small square box in the path. The temporal profile of this modulation is an initial rapid rise followed by a slower decay.

The basic JPSTH analysis of these "raw" data is shown in the left half of Fig. 4. At left and below the JPSTH matrix are the ordinary PST histograms of the two units. The abscissa PSTH (for unit 10) is repeated below the histogram grouping at the right of the matrix. Rising towards the upper right is the PST coincidence histogram and at the extreme right is the ordinary cross-correlogram.



Joint Peri Stimulus Time Histogram (JPSTH), Fig. 2 Bin arrangements for (a) JPSTH matrix, (b) peristimulus coincidence histogram, (c) cross-correlogram

The PST histograms show the time course of the stimulus-driven increase in firing. As expected from the descriptions of the scatter diagram construction and the simulated circuit used to generate the data, the JPSTH matrix shows a hill, a fairly broad stripe parallel to each axis, and a narrow stripe parallel (just above) the principal diagonal. The PST coincidence histogram shows a broad peak at the times when both neurons have stimulus-induced higher firing rates, which is otherwise fairly small. Finally the cross-correlogram shows a narrow peak near the origin riding on a flat background.



Joint Peri Stimulus Time Histogram (JPSTH), Fig. 3 Circuit used to generate spike trains with simulator program



Joint Peri Stimulus Time Histogram (JPSTH), Fig. 4 (Left) Matrix containing the raw spike coincidences (JPSTH) and the PST coincidence histogram (red) to the

Because the observed neurons are being co-modulated by the direct stimulus input, their firing rates increase and decrease in unison, thus creating a large part of the "raw" correlation structure. In order to infer "effective connectivity" or organization among our observed neurons, we need to compare the "raw" correlation to that expected for two independent neurons with precisely the observed PST histograms. This is accomplished with the corrected JPSTH as shown in the right half of Fig. 4. Here we subtract the matrix produced by the bin-by-bin product of the two PST histograms (divided by the number of stimuli) from the "raw" JPSTH matrix and then divide, again bin by bin, by the product of the standard deviations in each PST histogram. Each bin in the matrix has now become a correlation coefficient. PST histograms are shown as before, but the derived coincidence histogram and the cross-correlation are now corrected for firing rate changes (see entries ► "Significance Evaluation" and ► "Surrogate Data for Evaluation of Spike Correlation"). Note that the hill and bars parallel to the axes have disappeared from the corrected JPSTH matrix, while the diagonal stripe has persisted. The corrected PST coincidence histogram shows an initial rapid rise and subsequent slow fall, as expected from the stimulus modulation of the synaptic connection in the simulator. The corrected cross-correlogram shows only a central peak, with no "background" correlation.



right. The cross-correlogram is shown in orange. (Right) Same display as shown on the left but here for the normalized JPST

We note that this matrix-based correction of the cross-correlogram is somewhat different but more accurate than correction based on the more usual shift or PSTH-based predictor. Thus, this correction has extracted the (known) stimulus timelocked modulation of the "effective correlation" between the two neurons and has removed the direct correlation effects of the stimulus-related co-modulation of firing rates.

It is necessary to establish significance for the features shown in the corrected JPSTH and its associated histograms and also to deal with nonstationarity in the neural activity. Methods for both objectives have been worked out and are discussed in Palm et al. (1988) and Gerstein (1998). In addition it is not necessary to use square time bins in the JPSTH matrix. For example, the bin resolution perpendicular to the main diagonal can be much higher than along it. This produces a stimulus-locked and time-resolved crosscorrelation along the main diagonal (see Gerstein 1998; Aertsen 2021) for more detail). Please find an example application of the JPSTH in Vaadia et al. (1995).

## **Cross-References**

- Correlation Analysis of Parallel Spike Trains
- Estimation of Neuronal Firing Rate

- ► Significance Evaluation
- Surrogate Data for Evaluation of Spike Correlation

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