Bounds of the Ability to Destroy Precise Coincidences by Spike Dithering

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Abstract. Correlation analysis of neuronal spiking activity relies on the availability of distributions for assessing significance. At present, these distributions can only be created by surrogate data. A widely used surrogate, termed dithering, adds a small random offset to all spikes. Due to the biological noise, simultaneous spike emission is registered within a finite coincidence window. Established methods of counting are: (i) partitioning the temporal axis into disjunct bins and (ii) integrating the counts of precise coincidences over multiple relative temporal shifts of the two spike trains. Here, we rigorously analyze for both methods the effectiveness of dithering in destroying precise coincidences. Closed form expressions and bounds are derived for the case where the dither range equals the coincidence window. In this situation disjunct binning detects half of the original coincidences, the multiple shift method recovers three quarters. Thus, only a dither range much larger than the detection window qualifies as a generator of suitable surrogates.

Keywords: multi-channel recording, spike train, Monte-Carlo, surrogate data, correlation.

1 Introduction

The only way to identify information processing in biological neuronal networks is to simultaneously record from many neurons at a time. Nowadays multi-channel recordings are a standard technique in electrophysiological laboratories. Correlation analysis of such data has demonstrated that neurons exhibit correlated spiking activity on a fine temporal scale (ms precision) and in relation to the experimental protocol [1,2]. This has been interpreted as indicative for an involvement of correlated spiking activity in brain processing.

However, the presence of correlated spiking activity is not obvious from visual inspection. At first sight, the data appear to originate from a stochastic process with large variability in the number and the timing of spikes in responses to an identical stimulus. Furthermore, the rate of spike emission typically exhibits a
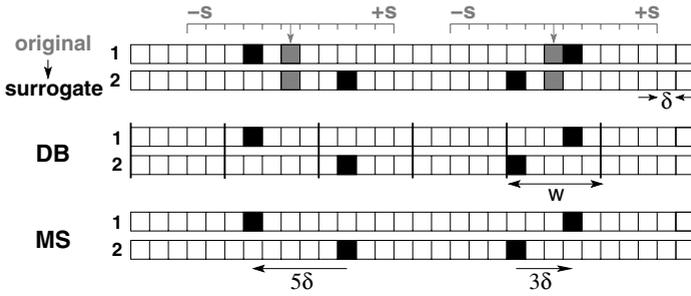
Fig. 1. Spike dithering and two methods of coincidence detection. Filled bins indicate spike occurrence, the width of the bins indicates the time resolution δ (typically 1 ms). Top: Generation of surrogate data. Original simultaneous spike data (grey bins) of neuron 1 and 2. Coincidences are assumed to be precise (within the same bin). In surrogate spike trains (black bins) all original spikes are independently dithered with uniform probability in the range $\pm s$ (in units of δ). Middle: In the disjunct binning (DB) method coincidences are detected in exclusive windows of width w to allow a temporal jitter of the spikes. Only spikes within the same window (between thick vertical lines) are counted as a coincidence. Bottom: In the multiple shift (MS) method spike coincidences are detected if the distance between spikes is smaller than or equal to an a-priori parameter (see Sec. 3).

complex temporal profile. Clearly, spike coincidences with millisecond precision can also occur as chance events. Thus, the empirical number of joint-spike events needs to be compared to the distribution of coincidence counts resulting from independent spike trains. This distribution can only be derived using strong assumptions about the statistics of the spike trains [3] typically not fulfilled by electrophysiological data. Therefore, Monte-Carlo methods are widely used to construct the distribution of coincidence counts from surrogate data [4] that maintain certain statistical properties of the original data but do not include correlations [5].

Various methods are in use for the generation of surrogate data [6,4,7,8,9]. All of them fulfill the condition to destroy the correlation, but also have the drawback to simultaneously destroy one or the other statistical feature of the data [8,10], e.g. the Poissonian nature or the exact spike counts. Date and colleagues proposed the method of spike dithering to generate surrogates which currently best meets the criterion to destroy the correlation between spike trains and simultaneously to maintain as many statistical properties of the data as possible [11]. The approach is to randomly re-place each spike within a small time window around its original position, thereby almost perfectly preserving the other statistical features of the single neuron data. Meanwhile, the method is in routinely use in the correlation analysis of neuronal spike trains [12,13]. Strategies have been developed to reduce the perturbation of the inter-spike interval statistics for moderate dithers [10,14].

However, it is not well understood how much dither is required to destroy the spike correlation, in particular if joint-spike events are allowed to have a temporal

jitter. Here we study the decay rate of the number of coincidences as a function of the dither width and as a function of allowed temporal jitter of the coincidences. In particular we answer the question to which degree coincidences are destroyed, if the dither width corresponds to the allowed temporal jitter of the joint-spike events. Intuition says that coincidences should then be reduced by 50%. This needs to be analyzed in the context of the chosen method of coincidence detection since it critically influences the result: we concentrate on the disjunct binning method (DB) and the multiple shift method (MS) of coincidence detection [15] (cf. Fig. 1 middle and bottom, respectively).

In the following we treat the two methods in two subsequent sections, in each of which we briefly introduce the respective method, and derive analytically the probability of detecting coincidences given originally precise coincidences as a function of dither and of the allowed coincidence width. The results section compares the two methods for the particular case of the applied dither being equal to the allowed coincidence width. We show that the probability of detection decays with increasing dither, however much faster for DB as compared to the MS method. We also compare to the case where only one spike train is dithered.

2   Disjunct Binning

The original spike data are discretized into bins of width δ, such that the total duration T of the recording is divided into N bins ($T = \delta \cdot N$). Each bin is assumed to contain at most one spike. As a result the activity of each neuron is represented by a binary sequence (Fig. 1) of zeros (no spikes) and ones (spikes). We define coincident events (or simply coincidences) as the joint firing of the two neurons within a coincidence window of w bins, thereby allowing coincidences to have a certain temporal jitter. In order to detect the total number of coincident events, the DB method sections T into disjunct, adjacent time segments (coincidence windows) $W_k, k = 1, ..., \lceil N/w \rceil$ each containing w bins of width δ. With bins numbered from 1 to N, the first coincidence window W_1 is composed of bins $\{1, 2, ..., w\}$, the second W_2 of $\{w + 1, w + 2, ..., 2w\}$, and so on.

We assume the original coincidences (i.e., before dithering) to be perfectly synchronous joint-events, i.e., both neurons have a spike in the very same bin. Due to an applied dither in the range of $[-s, s]$ bins a spike may trespass the border of a coincidence window and fall into another coincidence window. The *dither factor* $D = \lceil \frac{s}{w} \rceil$, i.e., the next integer larger than (or equal to) $\frac{s}{w}$, defines in how many coincidence windows the spike may fall and thus how many borders it might cross.

Next we are interested in the probability to detect a coincidence after dithering. The result depends on whether dithering is applied to both neurons (*2-neuron dithering*) or only one neuron (*1-neuron dithering*). The approaches are treated separately in the next two sections.

2.1   2-Neuron Dithering

In 2-neuron dithering each spike of both spike trains is randomly displaced in the range of $[-s, s]$ bins with uniform probability.

In order to calculate the probability that a coincidence after dithering is still detected as a coincidence, we need to consider all coincidence windows W_k into which the dithered spikes may be scattered. The number of windows is given by the dither factor D. If we assume the original coincidence to be in window W_0, spikes may be dithered into coincidence windows W_k with $k = 0, \pm 1, \pm 2, ..., \pm D$. Therefore, the probability is the sum of the probabilities that the spikes fall into the same window W_k.

The probability to detect a coincidence within a particular coincidence window W_k depends on the number of bins that may be reached from the original coincidence position given a particular dither s. The probability to fall in a single bin δ within the dither interval $[-s, +s]$ is $1/(2s+1)$. Depending on the initial position $\alpha = 1, 2, ..., w$ of a spike in the coincidence window, a different number of bins is reachable in the surrounding coincidence windows. In the coincidence windows where all w bins can be reached ($k \in [-D+2, ..., D-2]$), the probability of a spike to fall into the window is $\Delta w_k^\alpha \cdot \frac{1}{2s+1}$, with $\Delta w_k^\alpha = w$. In the remote windows $\{W_{-D}, W_{-D+1}, W_{D-1}, W_D\}$, the probability corresponds to the number of reachable bins, i.e., $\Delta w_{k'}^\alpha \cdot \frac{1}{(2s+1)}$ with $k' = -D, -D+1, D-1, D$, respectively.

Because the two coincident spikes are dithered independently, the joint probability of both spikes being in window W_k is the product of the probabilities $(\Delta w_k^\alpha \cdot \frac{1}{2s+1})$ for the individual spikes. Then the total probability to detect the coincidence after dithering is given by the sum of the joint probabilities across all reachable coincidence windows:

$$P_\alpha^{[2-n]}(w, s) = \sum_{k=-D}^{k=D} \left(\frac{\Delta w_k^\alpha}{2s+1} \right)^2 . \tag{1}$$

The closure relation is given by the condition that the total dither involves $2s+1$ bins:

$$\sum_{k=-D}^{k=D} \Delta w_k^\alpha = 2s+1 \quad \Rightarrow \quad \sum_{k=-D}^{k=D} \frac{\Delta w_k^\alpha}{2s+1} = 1 . \tag{2}$$

Fig. 2A,B show the coincidence detection probability $P_\alpha^{[2-n]}(w, s)$ as a function of the initial position α of the spikes in the coincidence window, for different values of the dither s. Surprisingly, the probability of detection $P_\alpha^{[2-n]}(w, s)$ depends on the distance of the initial coincidence from the borders of the coincidence window. For $s = w$ (Fig. 2A) the probability $P_\alpha^{[2-n]}(w, s)$ reaches its minimum if the initial coincidence is in the center of the window, and is maximal when the initial coincidence is just at the window border. This counterintuitive result holds true for all values of w. However, it can be understood by considering that if spikes were originally in the proximity of the border of the coincidence
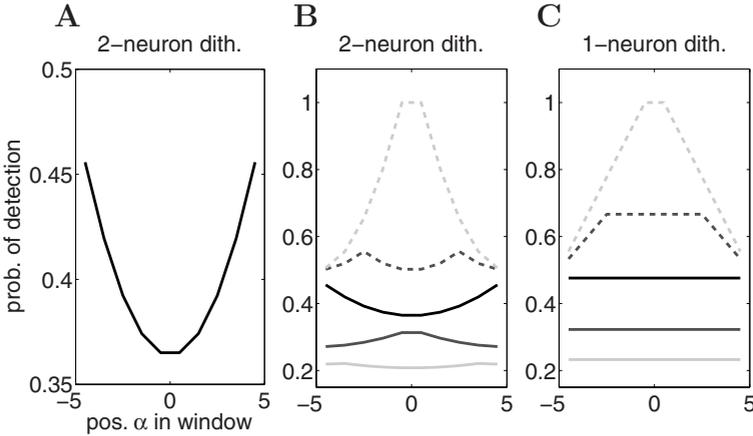
Fig. 2. Probability of detecting coincidences after dithering for DB as a function of the position α of the original coincidences measured from the center of the coincidence window W_0. A,B: For 2-neuron dithering. C: For 1-neuron dithering. Black curves: case $w = s$ (enlarged ordinate in A), solid grey curves: $w < s$, dashed grey curves: $w > s$. Parameter values: $w = 10$, $s = 15$ (solid, dark grey), $s = 21$ (solid, light grey), $s = 7$ (dashed, dark grey), and $s = 4$ (dashed, light grey).

window the number of destination windows is generally smaller than for originally centered spikes. As a consequence, spikes fall in larger stretches of successive bins, and thus the probability for the fission of coincidences by the borders of the coincidence windows is reduced. The total probability $P_\alpha^{[2-n]}(w, s)$, which is constrained by Eq. 2, is maximized if few increments Δw_k^α are large and is minimal if all increments have intermediate values. In other words, the number of ways of arranging the two spikes in a destination window increases quadratically with the number of involved bins (cf. Eq. 1), hence the α-dependance observed in Fig. 2A.

As shown in Fig. 2B, the overall probability $P_\alpha^{[2-n]}(w, s)$ progressively increases with decreasing s from $s > w$ to $s < w$, shown here for a fixed w. For decreasing s the spikes have a decreasing chance to trespass the window border and to escape from their original window. In extreme, for $s \ll w$ the spikes may not reach any other windows and thus stay coincident. In contrast, for $s > w$ the coincidence has an increasing probability to be destroyed because of the large number of potential destination windows. The probability $P_\alpha^{[2-n]}(w, s)$ shows different shapes depending on the exact relationship between s and w.

2.2   1-Neuron Dithering

In case only the spikes of one spike train are dithered (e.g. only the spikes of neuron 2, [6]) the probability of detecting the coincidences after dithering only depends on the new positions of the spikes of train 2. This method leads to a

total probability

$$P_\alpha^{[1-\mathrm{n}]}(w, s) = \begin{cases} w/(2s+1) & \text{if } s \geq w - 1 \\ \Delta w_k^\alpha/(2s+1) & \text{if } s < w - 1 \,, \end{cases} \tag{3}$$

where we assumed the initial coincidence window to be W_k and Δw_k^α to be the associated number of bins reachable by a spike from neuron 2. Again, this number depends on the initial position α of the spike.

For $s \geq w - 1$ both sides of the dither window $[-s, s]$ are larger than the coincident window W_k and thus the probability for the two original spikes to stay coincident after dithering depends on the probability for the dithered spike to stay in that window. Its probability is given by the number of bins in the window w relative to the total number of possible bins, i.e., $2s + 1$, the spike may be dithered into (upper relation in Eq. 3). This obviously does not depend on the initial position α of the coincidence.

If both sides of the dither window are smaller than the coincident window ($s < w - 1$), only a fraction of the bins may receive a spike after dithering and depends on the original position α of the spike (Fig. 2C). For $s < w - 1$ the probability of detecting the coincidence after dithering increases progressively as s decreases, with a maximum at the central bins of the window. The maximal detection probability $w/(2s + 1)$ is attained if the whole dither window $[-s, s]$ is included in the coincidence window W_k.

3   Multiple Shift

This method provides a different way of counting coincident spikes of two neurons, avoiding the arbitrarily located "hard" borders. The multiple shift method defines a maximum allowed shift b. Assuming again the spike trains to have resolution δ, the procedure begins with counting all precise coincidences. Then spike train 2 is shifted with respect to spike train 1 by δ and again all precise coincidences are counted. The procedure continues for all positive shifts $2\delta, 3\delta, .., b\delta$ and for the negative shifts $-\delta, -2\delta, ..., -b\delta$. Consequently, spikes with a distance of up to $\pm b$ bins are counted as coincident. The parameter b is analogous to the coincident width w, however with the substantial difference that there are no fixed borders and the initial position of the coincidence α is meaningless.

Consider both spikes constituting a coincidence to be dithered in the range $\pm s$ and the origin of the temporal axis to be located at the position of the initial coincidence. After dithering the probability to find spike 2 at distance k from spike 1 is given by the probability to find 1 at i times the probability to find 2 at $k + i$ summed over all possible positions i:

$$J(k, s) = \frac{1}{2s+1} \sum_{i=-s}^{s} p(k + i) \,. \tag{4}$$

However, $p(k+i)$ is subject to further constraints. If e.g. spike 1 is at $-s$, spike 2 can only be coincident or to the right of spike 1, requiring $p(k - s)$ to vanish for

negative k. Therefore, the effective limits of the sum also depend on k, collapsing Eq. 4 to

$$J(k,s) = \begin{cases} 1/(2s+1) & \text{for } k = 0 \\ \frac{2s+1-|k|}{(2s+1)^2} & \text{for } |k| \leq 2s \\ 0 & \text{for } |k| > 2s . \end{cases} \tag{5}$$

The probability of dithering two initially coincident spikes to a distance $|k|$ reaches its maximum at zero offset and decreases linearly with $|k|$ before it drops to zero at $\pm 2s$.

In the MS method all spikes dithered up to a distance $k = \pm b$ are classified as coincident. To obtain the probability to detect an initially coincident event after dithering $P^{[\mathrm{MS}]}(b,s)$ we have to sum the probabilities $J(k,s)$ of all possible dithering results for k in the range $-b, ..., b$

$$P^{[\mathrm{MS}]}(b,s) = \begin{cases} 1/(2s+1) & \text{for } b = 0 \\ \frac{1}{2s+1} + \sum_{k=-b}^{b} \frac{2s+1-|k|}{(2s+1)^2} & \text{for } b \leq 2s \\ 1 & \text{for } b > 2s \end{cases}$$
$$= \begin{cases} \frac{2b+1}{2s+1} - \frac{b(b+1)}{(2s+1)^2} & \text{for } b \leq 2s \\ 1 & \text{for } b > 2s . \end{cases} \tag{6}$$

4   Results

In this section we will derive the expected probability of detecting a coincidence after dithering given a large number of coincidences occurring in the spike trains at random times.

In the disjunct binning framework the assumption of many coincidences occurring at random times implies that the original coincident events will cover, in expectation, all possible initial positions $\alpha \in [1, ..., w]$. Therefore we have to average the results of Secs. 2.1 and 2.2 (Eqs. 1, 3) over α. For 2-neuron dithering this yields
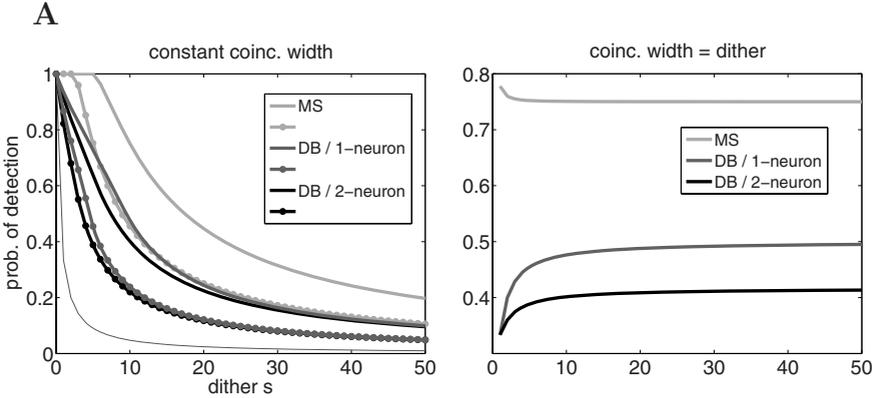
$$\langle P_\alpha^{[2-\mathrm{n}]}(w,s)\rangle_\alpha = \frac{1}{w} \sum_{\alpha=1}^{w} \sum_{k=-D}^{k=D} \left(\frac{\Delta w_k^\alpha}{2s+1} \right)^2 . \tag{7}$$

Using similar arguments we derive the expected probability for the case of DB after 1-neuron dithering utilizing Eq. 3:

$$\langle P_\alpha^{[1-\mathrm{n}]}(w,s)\rangle_\alpha = \begin{cases} w/(2s+1) & \text{if } s \geq w - 1 \\ \Delta w_k^\alpha/(2s+1) & \text{if } s < w - 1 , \end{cases} \tag{8}$$

whereas in the case of the MS method there is no α-dependence of the probability. For convenience however we also rewrite Eq. 6:

$$\langle P^{[\mathrm{MS}]}(b,s)\rangle = \begin{cases} \frac{2b+1}{2s+1} - \frac{b(b+1)}{(2s+1)^2} & \text{for } b \leq 2s \\ 1 & \text{for } b > 2s . \end{cases} \tag{9}$$

Fig. 3. Expected probability of detecting coincidences with DB and MS as a function of dither range. $\langle P^{[\mathrm{MS}]}(b,s)\rangle$ (light grey), $\langle P_\alpha^{[1-\mathrm{n}]}(w,s)\rangle_\alpha$ (dark grey), $\langle P_\alpha^{[2-\mathrm{n}]}(w,s)\rangle_\alpha$ (black). A: Three values of constant coincidence width. Thin curve: $b=0, w=1$ (MS and 1-/2-neuron, respectively), thick curves with knobs: $w=b=5$, thick curves: $w=b=10$. B: Bounds for coincidence width corresponding to dither width, $w=s$ and $b=s$ respectively.

Fig. 3A shows $\langle P_\alpha^{[2-\mathrm{n}]}(w,s)\rangle_\alpha$, $\langle P_\alpha^{[1-\mathrm{n}]}(w,s)\rangle_\alpha$ and $\langle P^{[\mathrm{MS}]}(b,s)\rangle$ as functions of the dither s and for three different values of allowed coincidence width. The expected probability declines with increasing dither in all cases. Detecting only precise coincidences ($w=1$ or $b=0$, respectively) the dither has a strong effect and destroys coincidences already at small values of s.

With increasing coincidence width the different cases deviate from each other, the 2-neuron dithering being the more effective way of destroying coincidences. For $w=b=10$ the 2-neuron dithering destroys about 80% of the original coincidences for dither values of about $s=20$. In this situation, the 1-neuron dithering leads to similar but slightly higher probabilities of detection, whereas for a similar loss of detected coincidences with the MS method a dither of about $s=50$ is required.

Let us now investigate the special case in which the dither equals the coincidence width, i.e., $s=w$, in order to obtain closed form expressions and limits. For the 2-neuron dithering setting $w=s$ and dither factor $D=1$ reduces Eq. 7 to

$$\langle P_\alpha^{[2-\mathrm{n}]}(w=s)\rangle_\alpha = \frac{1}{w}\sum_{\alpha=1}^{w}\sum_{k=-1}^{k=1}\left(\frac{\Delta w_k^\alpha}{2s+1}\right)^2$$

$$= \frac{1}{3} + \frac{s(s-1)}{3(2s+1)^2}\ . \tag{10}$$

For non-zero values of dithering Eq. 10 assumes values between $1/3$ (for $s, w=1$) and $\frac{1}{3}+\frac{1}{12}$ (for $s, w \gg 1$), that is $\frac{1}{3} \leq \langle P_\alpha^{[2-\mathrm{n}]}(w=s)\rangle_\alpha < 0.41\bar{6} = P_{\mathrm{lim}}^{[2-\mathrm{n}]}$. Therefore $P_{\mathrm{lim}}^{[2-\mathrm{n}]}$ is the maximum probability of detecting a 2-neuron dithered coinci-

dence with the disjunct binning method when the dither equals the coincidence width.

For 1-neuron dithering Eq. 8 with $w = s$ is just

$$\langle P_\alpha^{[1-\mathrm{n}]}(w = s)\rangle_\alpha = \frac{s}{2s + 1} \ , \tag{11}$$

where the probability is larger than $1/3$ $(s, w = 1)$ and tends to $P_{\mathrm{lim}}^{[1-\mathrm{n}]} = 0.5$ for $s, w \gg 1$.

Finally for the MS method replacing $b = s$ in Eq. 9 yields

$$\langle P^{[\mathrm{MS}]}(b = s)\rangle = 1 - \frac{s(s + 1)}{(2s + 1)^2} \ , \tag{12}$$

bounded between $1 - 2/9 = 0.\bar{7}$ $(b, w = 1)$ and $P_{\mathrm{lim}}^{[\mathrm{MS}]} = 0.75$ (for $b, s \gg 1$), the difference being only about 4%. The above results are visualized in Fig. 3B.

5   Discussion

In this contribution we have rigorously analyzed the effectiveness of 2-neuron dithering for the disjunct binning and the multiple shift detection methods and for comparison also 1-neuron dithering for DB. The analysis is restricted to precise coincidences. Further studies are required to investigate the biologically more relevant case of jittered (i.e., imprecise) coincidences [15], the presence of background activity, and processes with a biologically realistic inter-spike interval statistics [10]. Nevertheless, the present study provides detailed new insight in the dithering process. After uniform 2-neuron dithering of coincident spikes, the distribution of spike distances $|k|$ is not uniform, favoring the survival of coincidences. Furthermore, in DB the probability of detection after dithering depends on the initial location of the coincidence in a complex manner.

We provide analytic expressions for the expected probability of detection in the different scenarios. In DB and MS the expressions reduce to simple closed forms for $w = s$ and $b = s$, respectively. Under these constraints we obtain in the limit $s \to \infty$ the bounds $P_{\mathrm{lim}}^{[2-\mathrm{n}]} = 0.41\bar{6}$, $P_{\mathrm{lim}}^{[1-\mathrm{n}]} = 0.5$, and $P_{\mathrm{lim}}^{[MS]} = 0.75$. These asymptotic values are monotonically approached. Thus, for 1-neuron dithering analyzed by DB the intuition that a dither width equal to the coincidence window destroys 50% of the coincidences is confirmed. For 2-neuron dithering the rate of destruction is slightly larger. Counter to intuition, for MS the effect is much less pronounced. At $b = s$ still $3/4$ of the coincidences survive. For example, with $b = 10$ and $s = 50$ the probability of detection still is at $P^{[MS]}(b, s) \simeq 0.2$. Thus, for detection methods like MS which essentially evaluate the central peak of the cross-correlation, a dither width much larger than the detection window is required to destroy a relevant fraction of the coincidences.

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