Favorable Recording Criteria for Spike Sorting

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1 Introduction

Spike sorting is the generic term used to describe the procedure for identifying spikes in multi-neuron recordings and categorizing them according to waveform and amplitude differences. Correctly relating each spike to a category and accurately estimating its time of occurrence is prerequisite to processing recordings to determine individual and joint response properties of neurons.

Several phenomena complicate the detection, classification and time-of-occurrence estimation steps of the sorting procedure. We expect that all spikes will have very similar waveforms since they are governed by the same biophysical laws of Hodgkin-Huxley. Knowing the waveforms of recorded action potentials enhances detection—identifying that a spike occurred in the presence of noise—but their similarity means that classification—relating a spike to a neuron—becomes a difficult problem. Luckily, slight variations in spike shape and amplitude due to differing geometries of the neurons producing the spikes and their differing distance from the recording electrode simplifies spike sorting issues.

When spikes from different neurons overlap in time, both classification and detection become more difficult. For example, spikes from different units can negate each other, partially obliterating the spike and thus making detection more difficult, or they can enhance each other, resulting in a waveform that resembles neither, particularly in amplitude [1]. This paper characterizes the theoretical limits to which spikes can be correctly categorized, overlapping or not.

2 Spike Signal Constellation Model

We model spike sorting as a problem in signal detection and construct a signal constellation model for the recorded spikes. A signal constellation shows how the various choices of spike occurrences are related geometrically and portrays likely confusions among the possibilities. Here, we consider the simplest case of two neurons producing spikes recorded in a noisy background. We make the assumption that the neural recording is temporally segmented, with each segment short enough so that no single neuron produces two spikes within any segment. Any spike sorting algorithm has four choices for the best description of the observations: (i) spike 1 alone, (ii) spike 2 alone, (iii) both spikes, and (iv) no spikes. The constellation represents these four possibilities geometrically. In this problem formulation, detection and classification issues are decided simultaneously. Once classified, the time(s)-of-occurrence of the spike(s) are measured. We do not consider this aspect of the problem here.

We use the signal constellation idea to quantify how easy it is to detect and distinguish spikes from two different neurons with an *optimal* strategy. The optimal strategy relies on template

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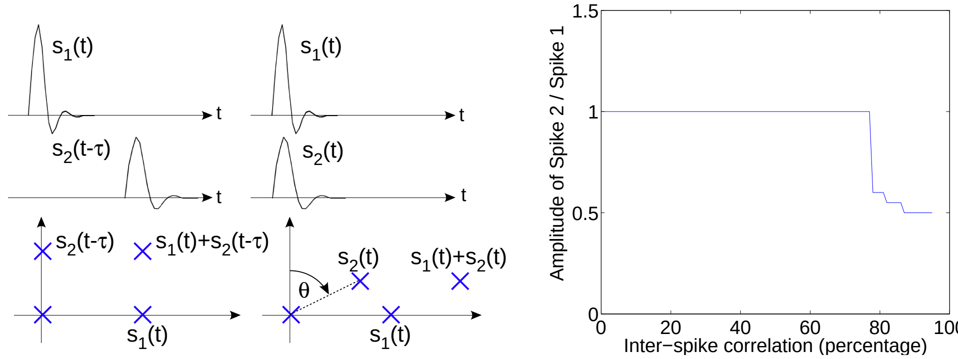

(a) (b)

Figure 1: (a) Constellation for non-overlapping spikes separated by a time delay τ (left side) and completely overlapping spikes (right side). Distance from the origin of s_1 and s_2 represents the respective amplitudes A_1, A_2 of the two spikes, and their geometric sum corresponds to the constellation point representing both spikes occurring within the observation window. (b) The optimal amplitude of spike 2 with respect to spike 1 that produces the smallest maximum classification errors varies with inter-spike correlation. Note the precipitous drop once a critical correlation value is reached.

matching followed by subsequent processing that disambiguates overlapping spike waveforms. Both temporal overlaps and similar waveform morphology contribute to errors. As shown in the left half of Figure 1(a), when the two neurons' spikes do not overlap at all, they are orthogonal. When the spike waveforms begin to overlap, they are no longer orthogonal and the constellation changes to a parallelogram having sides of the same lengths as in the original rectangle. Distance between constellation points qualitatively shows which models will confound each other. The rectangle⟶parallelogram constellation change induced by spike overlap will tend to make spike 1 and spike 2 be confused with each other.

Geometrically, the correlation angle θ that marks the parallelogram's slant equals $\sin^{-1}\rho$, where ρ is the inter-spike cross-correlation for a given overlap τ.

$$\rho = \frac{\int_0^T s_1(t)s_2(t-\tau)\,dt}{\sqrt{\int_0^T s_1^2(t)\,dt \cdot \int_0^T s_2^2(t-\tau)\,dt}}$$

At complete overlap, spikes having identical waveforms, even when they have different amplitudes, will be perfectly correlated and all constellation points will lie on the horizontal axis. If the waveforms differ, being aligned in time still produces the maximal correlation, but it is not one. The right half of Figure 1(a) illustrates this situation.

We use our spike signal constellation model to analyze detection and classification errors to determine recording criteria that allow the smallest theoretically possible errors. While we can never hope for an omniscient template-based classifier in spike sorting, results derived using the optimal detectors performance characteristics lend insight into which recording situations are most favorable.

We determined the spike amplitude combinations that minimize the maximum detection error. For this calculation, spike 2 is defined to have the smaller amplitude ($A_1 \geq A_2$) and we minimize the occurrence of the most likely error event, namely, saying that a single spike, say spike 2, occurred when actually one of the other three descriptions is correct. When the spikes do not overlap at all, thus making the correlation zero, we calculate that equi-amplitude spikes comprise the optimal amplitude distribution. This result makes sense since we would like non-overlapping spikes to be as large as possible to detect them easily. On the other hand, when perfect correlation occurs ($\theta = \pi/2$ and the spikes are identical and aligned in time), spike 2 lies on the same axis as spike 1. In this case, $A_2 = A_1/2$ is the optimum solution that minimizes error. Between these extremes, increasing spike waveform overlap causes a non-zero correlation, which makes the maximal correlation angle θ differ from zero. Up to some critical angle θ_c, we find that minimum error is still achieved when $A_2{=}A_1$ (see Figure 1b). However, when correlation angle increases beyond θ_c, the A_2 value for minimum error jumps abruptly to values close to $A_1/2$, and equals $A_1/2$ when $\theta = \pi/2$. Surprisingly, *there is no smooth transition.* The θ_c at which this drop occurs is dependent on the signal-to-noise ratio (SNR) of the recording; the higher the SNR, the greater θ_c. Thus, for the minimax error criterion, it is optimal to select neural recordings that produce spikes of equal amplitude, unless the spikes have extremely similar waveforms.

3 Conclusion

When spikes from different neurons overlap in time, the degree of correlation determines the optimal recording situation. Little overlap suggests equi-amplitude recording, while highly correlated discharges demand one amplitude be half the other (in the case of two neurons). This guideline also applies when more than two neurons are being extracted from the recording. The correlation is determined by the spike templates, which some spike sorting algorithms use directly. Even in cases of high correlation due to temporal overlap and/or waveform similarity, we can rely on amplitude differences to separate spikes. Conversely, two totally overlapping equi-amplitude spikes can be optimally sorted if their waveforms differ enough (i.e., how much less than one is their maximal cross-correlation).

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