Pattern Filtering for Detection of Replayed Patterns in HVc Sleep Activity[§]

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Abstract. Consolidation of memories during sleep may involve neuronal replay of daytime activity patterns. A precise replay phenomenon was observed in the song system nucleus RA. We developed statistical pattern filtering to investigate replay in HVc, where spiking activity is more variable. Long spike sequences during sleep were convolved with filters constructed from exemplar auditory spike sequences. Examining peaks in the filter responses, we found many examples of HVc spike trains with temporal patterns similar to the exemplars, confirming a replay phenomenon for HVc. Statistical pattern filtering has general utility for finding spike patterns when a referent pattern is known.

Introduction   In the zebra finch forebrain nucleus robustus archistriatalis (RA), neurons generate sequences of spike bursts during spontaneous sleep activity that exhibit similar temporal patterns as the pre-motor activity during singing and the auditory responses to song playback in the sleeping animal [2, 3, 11]. This sleep replay phenomenon is hypothesized to play an important role in learning and memory consolidation of the birdsong system [2, 7], which gives rise to the question of whether and how other parts of the song system participate in replay during sleep. The forebrain nucleus HVc is a sensorimotor center of the birdsong system. It projects to RA, and is thought to play an important role in vocal learning, auditory input integration, and higher level motor command. State-dependent auditory responses have also been observed for the HVc [9, 10]. We thus investigated whether the replay phenomenon also occurs in spontaneous sleep activity of HVc.

Instead of searching for individual replayed spike bursts [2], our goal was to find burst sequences that have similar temporal patterns as pre-motor activity or auditory responses [6, 8]. This is challenging for two reasons. First, unlike pre-motor or auditory data, for sleep spontaneous neuronal data, there are no reliable observables to mark the occurrence of neuronal events of interest. Second, the neuronal activity in HVc has far more variability than RA activity.

Pattern filtering   We developed a so-called pattern filtering methodology to address the above difficulty. In general, let Z be an exemplar spike train with spikes registered at $z_1 < z_2 < \cdots < z_p$, $z_k \in [0, \sigma]$. Fix $K(x) \geq 0$ and $B(x) \leq 0$, with $K(x) > 0$ only for $x \in (-\epsilon, \epsilon)$. The functions will be referred to as the "time window function" for a spike and the "background function", respectively. Define F on $[0, \sigma]$ by

$$F(x) = \begin{cases} \max_{1 \leq k \leq p} K(x - z_k) & \text{if } x \in \bigcup_{k=1}^{p}(z_k - \epsilon, z_k + \epsilon) \\ B(x) & \text{otherwise} \end{cases} \tag{1}$$

Let T be a long sequence of spikes at $t_1 < \cdots < t_N$, $t_k \in [0, \tau]$. Regard T as a series of δ functions, i.e., $T(x) = \sum_{i=1}^{N} \delta(x - t_i)$. Define R on $[0, T]$ by

$$R(x) = \int_0^\sigma F(s)T(x + s)\, \mathrm{d}s. \tag{2}$$

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Given fixed threshold $\theta > 0$, we then search for local maximum points $x_1, \ldots, x_l$ of $R(x)$ with $R(x) \geq \theta$ and output them as plausible locations in T where spike sequences similar to S occur.

The search proceeds rapidly because R is the linear convolution between $\Phi(s) := F(-s)$, $s \in [-\sigma, 0]$ and T, which can be computed efficiently by the fast Fourier transform, leading to quick detection of plausible patterns from T. We refer to Φ as the *pattern filter* associated with Z, and the convolution **pattern filtering**.

The underlying statistical model Pattern filtering is a likelihood ratio hypothesis test, as opposed to likelihood test in the unitary event analysis [4, 5]. It is based on three statistical assumptions. First, each spike sequence is generated randomly either conditional on a sequence $\{z_1, \ldots, z_p\}$ ("target pattern"), or a symbol "background". Second, spikes in the sequence are *conditionally independent*, such that (1) given the sequence being generated by the target pattern, the spiking probability is p_0 at each location in $J := \bigcup_{k=1}^{p}(z_k - \epsilon, z_k + \epsilon)$, and q_0 at each location outside J, and (2) given the sequence being generated by the background, the probability is q at any location. Third, and naturally, $p_0 > q \geq q_0$.

Let T be as previous. Given x, let $S \subset T$ consist of spikes in $[x, x + \sigma]$. Register S on the same time frame as the target pattern. If n spikes of S fall inside J, and m outside, then it is not hard to show

$$L(S) := \log \frac{P(S|target)}{P(S|background)} = \log \frac{p_0^n q_0^m}{q^{n+m}} = n\alpha - m\beta, \ \alpha = \log \frac{p_0}{q} > 0, \ \beta = \log \frac{q}{q_0} \geq 0 \qquad (3)$$

Define F by (1), with $K(s) = \alpha$ for $s \in (-\epsilon, \epsilon)$ and 0 for $s \notin (-\epsilon, \epsilon)$ and $B(s) \equiv -\beta$. Then $L(S) = R(x)$ as in (2). Since x is arbitrary, R consists of the log-likelihood ratios at all locations in T. Thus, by locating peaks in R with values larger than a given threshold, plausible patterns similar to the target are detected.

Note that the assumption of conditional independence is *not* an assumption of independent firing. Moreover, it can be shown that both the "sliding sweeps" algorithm [1, 8] and the cross-correlation method [2, 6] can be implemented by pattern filtering. Finally, it is straightforward to generalize pattern filtering to multiple units, incorporating spatial as well as temporal structure of neural activity.

Preliminary Results We implemented pattern filtering for HVc single unit data recorded during sleep. In most cases, it took less than 5 seconds to process a spike train of 10 minutes duration. In the example illustrated in the figure to the right, there were 126 responses collected while the bird's own song was broadcast to the sleeping bird (Fig. A). Note the variability in the response. These responses were used to make a bank of pattern filters representing the response to the motif in the song. These filters were subsequently applied to recordings of the same neuron collected when no acoustical stimulus was presented. From a total of approximately 15 minutes of recordings of spontaneous activity, we detected 33 exemplars of spontaneous activity whose filter responses were high enough.

A

B
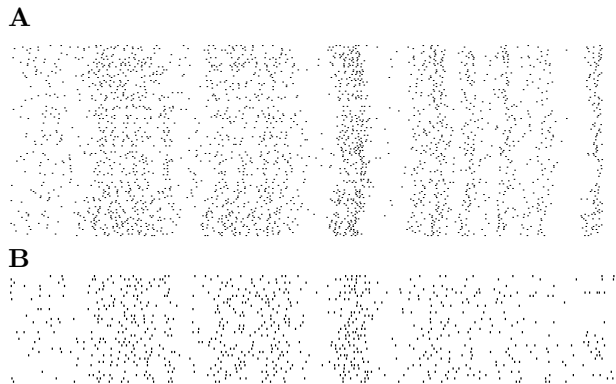
(All spike sequences are 580 ms long)

These are displayed in Fig. B. Note the similarity of matching between the response to BOS and the spontaneous spike sequences. This is the first quantitative evidence that replay during sleep occurs in a song system nucleus other than RA.

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