Available at
www.ComputerScienceWeb.com
POWERED BY SCIENCE DIRECT®

NEUROCOMPUTING

Neurocomputing 52–54 (2003) 19–24

www.elsevier.com/locate/neucom

Detection of spike patterns using pattern filtering, with applications to sleep replay in birdsong

Zhiyi Chi[a,*], Peter L. Rauske[b], Daniel Margoliash[b]

[a] *Department of Statistics, University of Chicago, 5734 University Avenue, Chicago, IL 60637-1514, USA*

[b] *Department of Organismal Biology and Anatomy, University of Chicago, 5734 University Avenue, Chicago, IL 60637, USA*

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.

Keywords: Pattern recognition; Sleep; Birdsong; HVc

1. 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]. 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

* Corresponding author.
E-mail address: chi@galton.uchicago.edu (Z. Chi).

0925-2312/03/$ - see front matter
doi:10.1016/S0925-2312(02)00746-4

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.

2. Pattern filtering

We developed a statistical methodology using linear filtering to address the above difficulty. In general, let S be an exemplar train of spikes registered at $s_1 < s_2 < \cdots < s_p$, $s_k \in [0, \sigma]$. Given a small number $\varepsilon > 0$, fix two functions $K(x)$ and $B(x)$, with $K(x) \neq 0$ only for $x \in (-\varepsilon, \varepsilon)$ and $B(x) \leqslant 0$ for all x. The functions will be referred to as the "time window function" for a spike and the "background function", respectively, and ε the "window size". Define F on $[0, \sigma]$ by

$$F(x) = \begin{cases} \max_{1 \leqslant k \leqslant p} K(x - s_k) & \text{if } x \in J_S, \\ B(x) & \text{otherwise,} \end{cases} \tag{1}$$

where

$$J_S = \bigcup_{k=1}^{p} (s_k - \varepsilon, s_k + \varepsilon). \tag{2}$$

Let T be a data sequence of spikes registered at $t_1 < \cdots < t_N$. Regard T as a series of δ functions, i.e., $T(x) = \sum_{i=1}^{N} \delta(x - t_i)$. Define function R by

$$R(x) = \int_0^{\sigma} F(s)T(x + s)\,\mathrm{d}s. \tag{3}$$

We then search for local maximum points of R with super-threshold values and output them as plausible locations of targets, namely segments of T with temporal patterns similar to S. More specifically, given $r_0 > 0$ and $\theta > 0$, with $r_0 \approx 20$ ms in our study, each target location x satisfies $R(x) \geqslant \theta$ and $R(x) \geqslant R(t)$ for all $t \in (x - r_0, x + r_0)$ and the spike sequence in $[x, x + \sigma]$ is considered a potential target. To avoid overlapping segments to be output as targets, if $x_1, \ldots, x_n$ are plausible target locations with $I_i = [x_i, x_i + \sigma]$ intersecting with each other, we only choose one I_i, such that $R(x_i)$ is the largest among $R(x_1), \ldots, R(x_n)$.

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

In all the cases we studied, K and B also satisfied the following conditions: (1) K is symmetric on $(-\varepsilon,\varepsilon)$, and decreases as x increases from 0 to ε; (2) $K(x)\geqslant 0$ on most part of $(-\varepsilon,\varepsilon)$, except for x close to the boundary of the interval; (3) $\min\{K(x)\colon x\in(-\varepsilon,\varepsilon)\}\geqslant\max\{B(x)\}$; and (4) $B(x)\equiv c$ for some constant $c\leqslant 0$. All the conditions can be justified by an appropriate statistical model and at the same time simplify the computation.

3. The underlying statistical model

Pattern filtering is a likelihood ratio test, as opposed to likelihood test in the unitary event analysis [4,5]. To illustrate, consider the simplest filter constructed from the time window function $K(x)\equiv\alpha>0$, $x\in(-\varepsilon,\varepsilon)$, and the background function $B(x)\equiv-\beta\leqslant 0$. Then (3) leads to $R(x)=\#\{t_i\in T\cap[x,x+\sigma]\colon t_i-x\in J_S\}\times\alpha-\#\{t_i\in T\cap[x,x+\sigma]\colon t_i-x\notin J_S\}\times\beta$. Because $J_S\subset[0,\sigma]$, the formula is simplified into

$$R(x)=\#\{t_i\in T\colon t_i-x\in J_S\}\times\alpha-\#\{t_i\in T\colon t_i-x\notin J_S\}\times\beta.$$

Detection using this filter is derived from three statistical assumptions. First, each spike sequence is generated randomly either by the exemplar sequence $S=\{s_1,\ldots,s_p\}$ ("template") or by the background. Second, spikes in the sequence are *conditionally* independent, such that

(1) given the sequence being generated by the template, at any location within distance ε from a template spike, the probability of a spiking event is p_0, while at any other location, the probability is q_0;
(2) given the sequence being generated by the background, the probability of a spiking event is q everywhere; and
(3) conditioning on either case, the spiking events at different temporal locations are independent from each other.

Finally, $p_0>q\geqslant q_0$. In other words, compared to background activity, in activity generated by the template, spikes are more likely to occur around template spikes, and less likely to occur elsewhere.

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

Returning to the filtering procedure, let T be a data spike sequence. Given x, let T_x consist of the spikes of T in $[x,x+\sigma]$. Shift the spikes in T_x by x, so that the sequence is registered onto $[0,\sigma]$, the same time frame as the template S. If n spikes of T_x fall inside J_S, and m outside J_S, and the total duration of J_S is τ, then it is not hard to get the following likelihoods

$$p_o(T_x):=P(T_x\mid T_x\text{ generated by }S)=\mathrm{e}^{-p_0\tau-q_0(\sigma-\tau)}p_0^n q_0^m$$

$$p_a(T_x):=P(T_x\mid T_x\text{ generated by background})=\mathrm{e}^{-q\sigma}q^{n+m}.$$

Hence the log-likelihood ratio

$$L(T_x) := \log \frac{p_o(T_x)}{p_a(T_x)} = \log \frac{p_0^n q_0^m}{q^{n+m}} + C_S = n\alpha - m\beta + C_S, \tag{4}$$

where

$$\alpha = \log \frac{p_0}{q} > 0, \quad \beta = \log \frac{q}{q_0} \geqslant 0$$

and $C_S = -p_0\tau - q_0(\sigma - \tau) + q\sigma$ is a constant which only depends on the template S.

Therefore, if we define F by (1), with $K(x) = \alpha$ for $x \in (-\varepsilon, \varepsilon)$ and 0 for $x \notin (-\varepsilon, \varepsilon)$ and $B(x) \equiv -\beta$, then $L(T_x) = R(x) + C_S$. Since x runs across the entire time interval of the data spike sequence T, R consists of the log-likelihood ratios plus a constant of all the segments of T with the same duration as the template. Thus, by locating peaks in R with values larger than a given threshold, one can find all the segments that are significantly more likely to be a target than be part of the background.

4. Results

We implemented pattern filtering for HVc single unit data recorded during sleep. For each unit, the spike sequences in response to the bird's own song ('BOS') broadcast to the sleeping bird in multiple trials were selected as templates. Then, in the subsequent spontaneous activity of the unit when no acoustical stimulus was presented, segments with similar temporal patterns as the templates were searched. For the neuronal activity in HVc, several types of variability have to be taken into account: (1) the across-trial variability of the auditory response, which leads to differences across the templates; (2) the possible modulations in the time scale of the neuronal activity [8,2,6], which lead to time compression or expansion of potential targets; and (3) the transient change in firing rates, which may lead to false detections. To address the variability, we adopted a procedure involving multiple filters, time scales, and tests on the statistical significance of the targets. In most cases, it took less than 5 s to conduct detection for a spike train of 10 min duration using a single filter, thus the multi-level detection procedure was still computationally efficient.

In the example illustrated in Fig. 1, the first spike train in each group is a template, consisting of *all* the spikes during a rendition of the same "motif" (sequence of syllables) which lasted about 650 ms. The templates are aligned at the onsets of the renditions. The subsequent spike trains in each group are targets detected from the spontaneous activity, using filters constructed for the template. Since targets were detected at several time scales to account for possible time compression or expansion, they might have different durations than the templates. To make comparisons between the two, the targets are scaled in the plot, according to the scaling factors with which they were detected. For all the targets, the scaling factors are between 0.8 and 1.25. This example demonstrates the variability of the auditory response in HVc during sleep and that such variability may also be exhibited in the presumed "replay" during the spontaneous sleep activity.

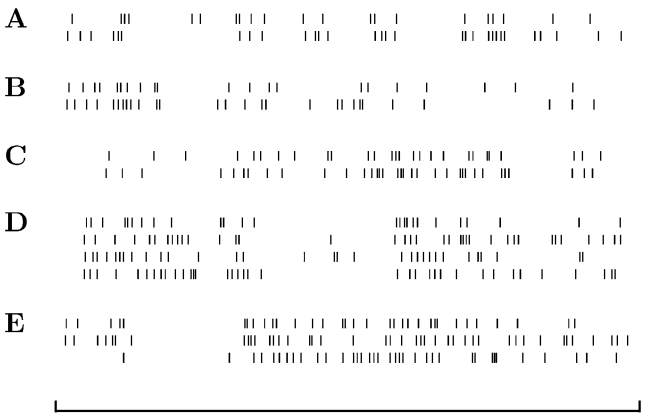

Fig. 1. Detection for a unit. In each group, the first spike train is a template and the others are targets detected using the filters for the template. The duration of a time interval (≈650 ms) during which a template was collected is illustrated at the bottom.

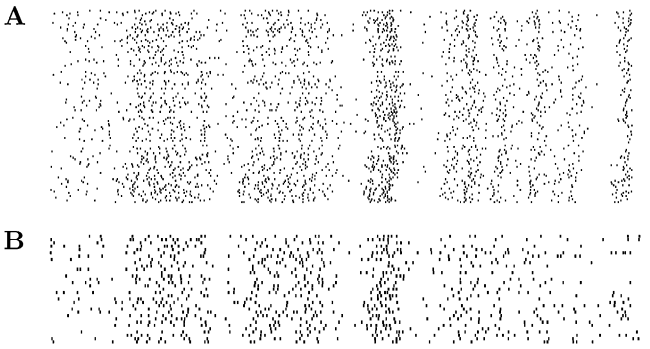

Fig. 2. Raster plots of templates (A) and detected targets (B). The targets in this case are not scaled, i.e., they have about the same duration as the templates (≈580 ms).

The second example is illustrated in Fig. 2. There were 126 responses collected while the BOS was broadcast to the sleeping bird (Fig. 2A). Again, the templates were associated with multiple renditions of a motif. While the responses were less variable than those in the previous example, they exhibited significant systematic change across the trials. For this unit, the detection was conducted without scaling the filters. From a total of approximately 25 min of recordings of spontaneous activity, we detected 33 exemplars of spontaneous activity. These are displayed in Fig. 2B. Note the similarity of matching between the responses to BOS and the spontaneous spike sequences. This example as well as the previous one is the first quantitative evidence that replay during sleep occurs in a song system nucleus other than RA.

References

[1] M. Abeles, G.M. Gerstein, Detecting spatio-temporal firing patterns among simultaneously recorded single neurons, J. Neurophysiol. 60 (1998) 909–924.
[2] A.S. Dave, D. Margoliash, Song replay during sleep and computational rules for sensorimotor vocal learning, Science 290 (2000) 812–816.
[3] A.S. Dave, A.C. Yu, D. Margoliash, Behavioral state modulation of auditory activity in a vocal motor system, Science 282 (1998) 2250–2253.
[4] S. Grün, M. Diesmann, A. Aertsen, Unitary events in multiple single-neuron spiking activity: I. detection and significance stimulus properties, Neural Comput. 14 (2002) 43–80.
[5] S. Grün, M. Diesmann, A. Aertsen, Unitary events in multiple single-neuron spiking activity: II. nonstationary data, Neural Comput. 14 (2002) 81–120.
[6] K. Louie, M.A. Wilson, Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep, Neuron 29 (2001) 145–156.
[7] D. Margoliash, Do sleeping birds sing? Population coding and learning in the bird song system, Prog. Brain Res. 130 (2001) 319–331.
[8] Z. Nádasdy, H. Hirase, A. Czurkó, J. Csicsvari, G. Buzsáki, Replay and time compression of recurring spike sequences in the hippocampus, J. Neurosci. 19 (1999) 9497–9507.
[9] T.A. Nick, M. Konishi, Dynamic control of auditory activity during sleep: correlation between song response and EEG, Proc. Natl. Acad. Sci. USA 98 (2001) 14012–14016.
[10] M.F. Schmidt, M. Konishi, Gating of auditory responses in the vocal control system of awake songbirds, Nat. Neurosci. 1 (1998) 513–518.

Zhiyi Chi entered Peking University, Beijing, China in 1989. He entered Brown University, Providence, Rhode Island in 1993. He received an Sc.M.from the Department of Mathematics the next year. In 1998, he graduated from the Division of Applied Mathematics with a Ph.D. for work on 'Probability Models for Complex Systems' under the supervision of Stuart Geman. Since then he has been Assistant Professor in the Department of Statistics at the University of Chicago. He is currently also a member of the Committee on Computational Neuroscience at the University of Chicago.

Peter Rauske studied physics at the University of Chicago, graduating in 1994. He is currently studying the neurobiology of birdsong production and learning using chronic recording techniques with Daniel Margoliash's group at the University of Chicago, where he is pursuing a Ph.D. in the Department of Organismal Biology and Anatomy.

Daniel Margoliash studied biology at the California Institute of Technology. After graduating in 1975 he entered the Bioinformation Systems program in Engineering Science at Caltech. Eventually joining the laboratory of Masakazu Konishi, he studied auditory responses in the birdsong system. He received an M.Sc. in 1981, and in 1983 he received his Ph.D. for work on 'Songbirds, Grandmothers, and Templates: A Neuroethological Approach'. After a brief postdoctoral fellowship with Nobuo Suga at Washington University, St. Louis, he joined the faculty of the then Department of Anatomy at the University of Chicago in 1986. He is currently Professor in the Departments of Organismal Biology and Anatomy & Psychology, and the Committees on Neurobiology & Computational Neuroscience at the University of Chicago.