Evidence for slow (2-10 Hz) and gamma frequency coherence between spike trains and local field potentials in the cerebellum

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Submitted to CNS 2002

Abstract

A method for detecting relationships between single-unit spike trains and local field potentials (LFPs) was developed and applied to recordings from rat cerebellum. LFPs were repeatedly filtered with a shifting frequency window. The resulting traces were transformed into peak-time point processes for comparison with spike trains using 'relative-phase' analysis (Chen and Nitz, submitted). Discharge of some Purkinje cells was phase-related to LFP oscillations in the 2-10 Hz and 30-50 Hz frequency ranges. This analysis method revealed hidden coherency between spiketrains and LFPs. The findings suggest that cerebellar activity is, to some extent, temporally organized according to both slow and fast rhythms.

Summary

The correlation of single-unit neuronal recordings to their associated LFPs is difficult to study because spike trains are discrete point processes and LFPs are continuous. Direct cross-correlation (spike-triggered averaging) of these mixed time series is not always appropriate because it requires averaging of multiple trials or time windows and can be dominated by the frequency having greatest power in the LFP. Thus, this method cannot determine the time-series of interactions between spike trains and LFPs and is incapable of measuring transient periods of coherence. Furthermore, fluctuations of LFP frequencies exhibiting relatively high spectral power can mask significant correlations at other frequencies.

For these reasons, we developed a novel method by which to study correlations between mixed time series more effectively. The method, 'relative-phase' analysis, was then used to address an outstanding question concerning cerebellar function. That is, is simple-spike discharge of Purkinje cells coherent, and at what frequencies, with population activity within the cerebellum as measure by the LFP?

Cerebellar, single-unit spiketrains of putative Purkinje cells and their associated LFPs were recorded using stereotrodes. Recordings were made as rats performed a simple shuttling task for food reward. LFPs were filtered with a shifting (0.5 Hz steps), narrow-range (2 Hz) frequency window. The filtered traces were then converted to point processes by determining peak times. The temporal relationship between these LFP "events" and single-unit action potentials were studied for each narrow frequency range. Relative phase analysis was used to determine the instantaneous phase relationship between the converted LFPs and single unit spike trains. Relative phase here is defined as the relative timing difference between two point processes normalized by the associated interval of one process. The time of each single unit action potential was assigned a normalized phase (from 0 to 1) based on its temporal position between two peak times of the LFP for each frequency range tested (0-50 Hz). Thus, for all frequencies between 0 and 50 Hz, an averaged plot of phase versus spike discharge can be generated. The phase associated with each spike can also be analyzed as a time series in which transient periods of phase-locking to one or more LFP frequencies may be found. Note that this method also bypasses potential artifactual cross-correlations that occur between two point processes when one or both exhibit a high level of rhythmicity (Perkel et al., 1967).

Strong phase relationships between spike discharge and particular LFP frequencies were found for some cells. In cells exhibiting activity coherent with the LFP, there was a strong tendency for phase relationships to be confined to the 2-10 Hz and/or 30-50 Hz frequency ranges. Notably, phase relationships were found for frequencies that did not stand out in power spectral analyses of the LFP or in autocorrelations of the spike train.

The findings indicate that relative-phase analysis as applied to combined spike train/LFP recordings is a useful tool to uncover hidden temporal relationships between single unit activity and activity of the larger cerebellar network of which they are a small part. Similar to what has previously been shown for neocortical (Gray and Singer, 1989) and hippocampal (Buzsaki, 2002) spiketrain/LFP recordings, we have found that the simple-spike discharge of putative Purkinje cells is organized, to some extent, relative to the timing of cerebellar population activity as measured by the local field potential. Notably, this finding is consistent with recent work demonstrating: 1. the existence of cerebellar neurons in lobule II which exhibit tonically rhythmic discharge patterns at either slow (approximately 4-6 Hz) or high (approximately 20-50 Hz) frequencies (Nitz and Tononi, 2000); 2. the presence of transient periods (5-8 consecutive spike intervals) during which seemingly arrhythmic cerebellar neurons discharge spikes at regular intervals (Walcott, Chen, and Nitz, 2001). The functional role of such coherence and the extent to which it pervades the entire cerebellar network remains to be determined.

Acknowledgments

Research supported by the Neurosciences Research Foundation.

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