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Research Report

A novel method for quantifying similarities between oscillatory neural responses in wavelet time–frequency power profiles

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ABSTRACT

Quantifying similarities and differences between neural response patterns is an important step in understanding neural coding in sensory systems. It is difficult, however, to compare the degree of similarity among transient oscillatory responses. We developed a novel method of wavelet correlation analysis for quantifying similarity between transient oscillatory responses, and tested the method with olfactory cortical responses. In the anterior piriform cortex (aPC), the largest area of the primary olfactory cortex, odors induce inhibitory activities followed by transient oscillatory local field potentials (osci-LFPs). Qualitatively, the resulting time courses of osci-LFPs for identical odors were modestly different. We then compared several methods for quantifying the similarity between osci-LFPs for identical or different odors. Using fast Fourier transform band-pass filters, a conventional method demonstrated high correlations of the 0–2 Hz components for both identical and different odors. None of the conventional methods tested demonstrated a clear correlation between osci-LFPs. However, wavelet correlation analysis resolved a stimulus dependency of 2–45 Hz osci-LFPs in the aPC output layer, and produced experience-dependent high correlations in the input layer between some of the identical or different odors. These results suggest that redundancy in the neural representation of sensory information may change in the aPC. This wavelet correlation analysis may be useful for quantifying the similarities of transient oscillatory neural responses.

Abbreviations: aPC, anterior piriform cortex; aPCvr, ventro-rostral region of the aPC; EOG, electro-olfactogram; FFT, fast Fourier transform; LFP, local field potential; LOT, lateral olfactory tract; OR, olfactory receptor; osci-LFP, oscillatory local field potential; PC, piriform cortex

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1. Introduction

In the sensory system, the neural representation of a given stimulant is coded by activation of a specific subset of receptors overlapping to varying degrees with those of other stimulants. This overlap creates a degree of redundancy in these neural representations. Because such redundancy in neural representations is likely to change at different stages of sensory information processing, quantifying the similarities and differences between neural response patterns in sensory neurons and higher brain centers is an important step in understanding sensory neural coding. Sensory systems generate oscillatory activities between related cortical regions and the thalamus, which acts (except in the olfactory system) to gate sensory input to the cortex and provide feedback from cortical pyramidal neurons. While stationary oscillatory activity is relatively simple to compare, the degree of similarity or difference in transient oscillatory responses is significantly more difficult to analyze.

Among the mammalian sensory systems, the olfactory system has one of the most highly diverse repertoires of receptors (olfactory receptors; ORs), which makes it ideal for quantifying various similarities and differences between oscillatory responses. In olfaction, transient oscillatory local field potentials (osci-LFPs) are induced in the olfactory bulb (Adrian, 1950; Bressler and Freeman, 1980; Chapman et al., 1998; Chabaud et al., 2000; Lam et al., 2000) and in the anterior piriform cortex (aPC) (Bressler and Freeman, 1980; Ketchum and Haberly, 1993; de Curtis et al., 1994; Chapman et al., 1998; Chabaud et al., 2000; Ishikawa et al., 2007). In this pathway (Ishikawa et al., 2007), as well as in the other sensory thalamocortical circuit (Bruno, 2011), strong feed-forward inhibition is present. Possible integration of OR signals in the aPC (Desmaisons et al., 1999; Kashiwadani et al., 1999; Stettler and Axel, 2009) appears to be mediated via input synchronization by the above feed-forward inhibition (Ishikawa et al., 2007; Sato et al., 2008, 2015) transferred through an OR-specific pathway (Mombaerts et al., 1996; Serizawa et al., 2006). This signal integration, when occurring between different but overlapping ORs, could markedly change redundancy in the neural representations. Odorants activated different overlapping subsets of ~1000 murine ORs (Buck and Axel, 1991; Malnic et al., 1999, 2004; Zhang and Firestein, 2002), whose signals could be integrated in the aPC pyramidal cells. For example, ORs for carvones are estimated to include 70 types, with >80% overlap between carvone enantiomers (Hamana et al., 2003). The most sensitive dorsal ORs are critical for the supersensitive discrimination of the enantiomers (Sato et al., 2015), and despite the high degree of overlap, mice can easily discriminate between the carvone enantiomers even at high concentrations.

Thus far, there are no published methods for quantifying the similarity of aPC oscillatory responses, despite the need to understand the mechanism and relationships underlying the change in redundancy of neural representations in the aPC. In an analog of the mammalian olfactory cortex, the insect mushroom body, sliding cross-correlations between unit responses and LFPs were analyzed to attempt to identify response synchrony (Stopfer et al., 1997; Perez-Orive et al., 2002), whereas one study analyzed the wavelet coefficients for spike trains in the insect anntenal lobe (Capurro, et al., 2014).

Here, we compared several methods for quantifying the similarity of aPC osci-LFPs between identical or different odors. We first tried conventional methods, including cross-correlations between frequency band components generated through fast Fourier transform (FFT) band-pass filters. We then tried a novel method of wavelet correlation analysis, using sets of logarithmic ratios of cross-correlations to auto-correlations at representative frequencies, and compared the data collected using conventional versus the wavelet methods.

2. Results

2.1. *Odor-evoked osci-LFPs in the aPC were not strictly phase-locked to the stimulus onset and were not stationary over the time window of interest*

Odor-evoked osci-LFPs were recorded in an *ex vivo* isolated whole brain with attached nose preparation (Ishikawa et al., 2007; Sato et al., 2008). We first examined the reproducibility of odor-evoked osci-LFPs in layer I of the aPC. Through repeated 1-s presentation of identical odors, osci-LFPs showed similar but somewhat distinct temporal profiles (Supplementary Fig. S1). Moreover, a pair of quite different odors (Lav and mc468) evoked dissimilar osci-LFPs. Osci-LFPs began during the odor presentation, before the peak of the receptor potential: electro-olfactogram (EOG) response (the lowest trace in Supplementary Fig. S1). To calculate the correlation coefficients of the temporal profiles of these osci-LFPs, we employed a 2.5-s time window that was comprised of the 1-s odor presentation and the following 1.5 s.

Correlations of the temporal profiles of osci-LFPs were not homogeneously high between identical odors (Supplementary Fig. S2A). In 3 of the 28 Lav pairs, and the only 0.1-Lav pair, the correlations were relatively high (0.7–0.74). The remaining 25 Lav pairs demonstrated intermediate correlations of 0.47–0.69, and the mc468 pair demonstrated a low value of 0.29. These low correlations between osci-LFPs for identical odors may have been caused by differences in the oscillatory phase angles. Superimposed traces revealed that oscillatory components demonstrated independent fluctuations in phase angles and oscillatory powers including a few synchronous cycles even between identical odors (Supplementary Fig. S3). Some of the phase-matching points are indicated in Supplementary Fig. S3 by daggers. These results indicate that odor-evoked osci-LFPs in the aPC are not strictly phase-locked to the stimulus onset, and are not stationary over the time window of interest. That is, these properties prevented traditionally derived correlations of the temporal profiles from demonstrating the stimulus dependency of the osci-LFPs. Next, to identify the origin of the high correlations that were obtained between some of cases, we analyzed the contribution of different frequency components.