A wavelet method for comparing neural ensemble responses based on synchronization properties

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Recent modeling studies from our group have addressed the potential computational role of synchrony within neural ensembles for the representation and learning of odor stimuli in the honeybee olfactory system (Linster and Cleland, 2001; Cleland and Linster, 2002). Results from these studies suggest that spike synchronization among subsets of odor-responsive secondary olfactory neurons may serve to discriminate odors that evoke responses in highly overlapping populations of neurons. We have also shown that certain features of the stimulus, e.g., concentration or behavioral salience, can influence the synchronization properties of the olfactory processing network. Briefly, we suggested that the degree of synchrony among secondary olfactory neurons could directly reflect, and be modulated by, the behavioral relevance (salience) of the odor stimulus. Consequently, stimulus discriminability, which in these studies was directly dependent on synchronization properties, could also be modulated by parameters like behavioral relevance. Additionally, for a given degree of synchrony among secondary olfactory neurons, the read-out properties of the postsynaptic neuron could be modulated in such a way as to detect either only very tightly or more broadly synchronized events. Modulation of the postsynaptic read-out function would thus also modulate stimulus discriminability.

In these modeling studies, synchrony among spike trains was indirectly assessed via hebbian learning rules which favored the detection of synchronous events converging upon a postsynaptic element (Song, Miller and Abbott, 2000). Consequently, odor discrimination in these models depended largely on the specific parameters of the hebbian learning rules employed. In order to test our theories using spike trains derived from electrophysiological recordings, as well as those derived from computational models, we have developed a method to assess the synchronization properties of neural ensembles consistently and replicably without reliance on prior knowledge of such arbitrary parameter

sets. This method enables construction of distance measures between dynamically defined subsets of spike trains based on spike synchronization patterns within an ensemble.

Methods

We utilize a wavelet-based synchrony metric to measure the synchronization properties of ensembles of neural spike trains. Wavelet analysis is essentially a generalization of classical Fourier techniques, in which the space onto which signals can be projected includes functions that are time-localized, irregularly shaped and non-sinusoidal. This time-localization property, in particular, proves useful in decomposing signals that are nonstationary, aperiodic, and/or apparently chaotic, particularly in efforts to quantify the approximately coincident occurrence of temporal transients (e.g., neural spikes). For present purposes, a wavelet decomposition can be considered as the projection of a signal onto a space defined by a selected, incrementally-shifted, real-valued, time-localized function over a range of biologically feasible scales. A continuous wavelet transform (CWT) of a signal, using a selected wavelet function at a given scale, is performed by deriving a set of coefficients representing the degrees of correspondence between the signal and the finite wavelet shape as the wavelet is shifted incrementally over the domain of the signal. The coefficients derived from this transform are temporally specific, whereas those of the classical Fourier transform are temporally global (although highly localized in the frequency domain).

Application of our synchrony metric for a stimulus-activated ensemble of neurons thus proceeds as follows:

(1) CWT coefficients are derived from each spike train in the ensemble, and from the local field potential (LFP), using the 'coiflet5' wavelet (see Figure 1). This process is repeated for each of a range of scales between 0.5 and 300.

(2) The degree of synchronization between each spike train *i* and the ensemble in which it is embedded is then assessed at each scale by calculating the coefficient of correlation between the wavelet coefficients for spike train *i* and the smoothed LFP. For ensembles of size *n*, consequently, a full ensemble response synchrony characterization generates a single *n*-dimensional vector (at each scale), with elements in the interval [-1,1].

(3) The correlation coefficient between the *n*-dimensional vectors characterizing two ensemble responses at a given scale then indicates the similarity of the two responses (e.g., to two different stimuli) in terms of their spike synchronization properties.

Correlation coefficients are utilized due to their scale and shift invariance; they provide a reasonable measure of how the wavelet coefficients for one signal scale with those for another (i.e., the degree to which these two signals' correspondence with a given localized waveform covaries over time).

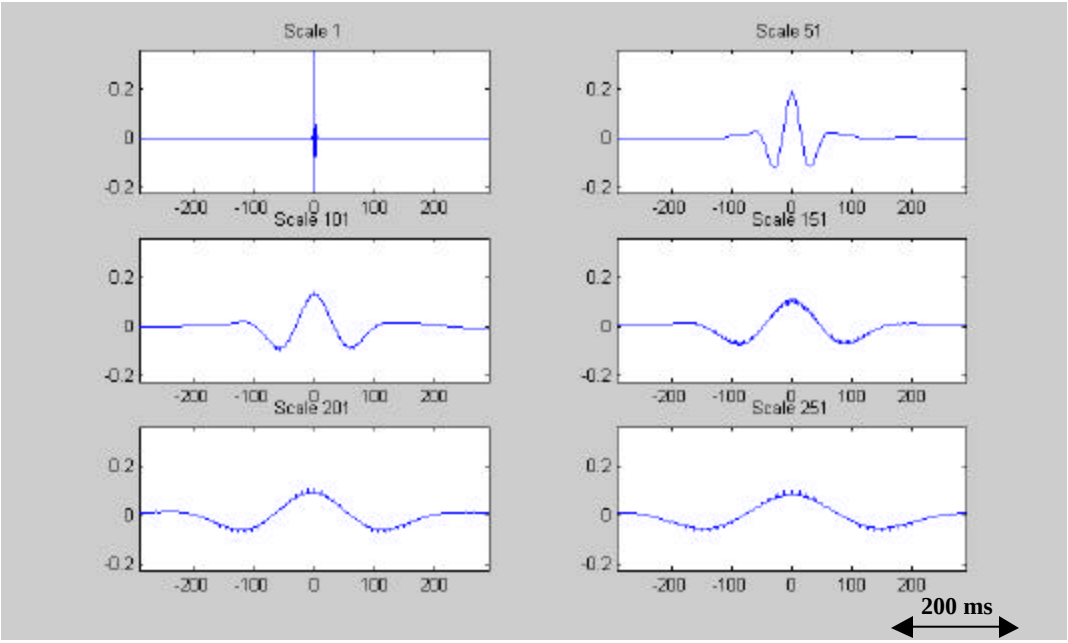

Figure 1. Depiction of "coiflet5" at increasing scales. *Abscissa*, milliseconds.

Application

Using our previously developed abstract model of the honeybee antennal lobe (AL) (Linster and Cleland, 2001), we tested these wavelet-based similarity calculations using spike trains generated in response to different odor stimuli. The reduced model consists of a population of 60 AL neurons that constitutively fire at a mean rate of 30 Hz. The mean firing rate of each individual neuron (on the timescale of seconds) is independent of afferent input; however, the firing pattern on a finer timescale is affected by odor application (see Figure 2). For any given odor, three adjacent model neurons are most strongly influenced by its application and are collectively termed the *odor focus*. Each neuron is also influenced to a lesser degree by odorants with qualities slightly different than that to which it is primarily attuned. The arbitrarily large dimensionality of odor quality variation is condensed into one hypothetical dimension of odor quality; model neurons are aligned along this circular axis according to their response spectra to odor stimuli. Thus,

any given odorant stimulus influences a one-dimensional neighborhood of neurons, with the odor focus located in the center of the affected population. The distance between two odor foci is an index of the similarity between those two odorants.

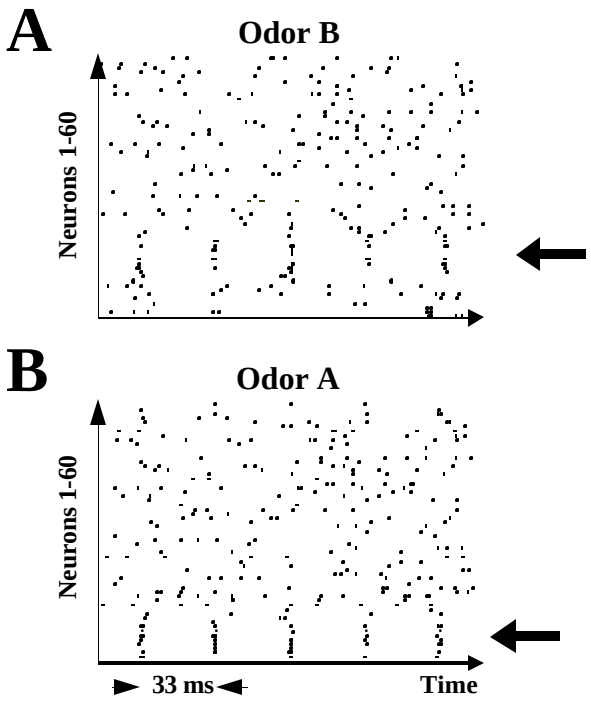

Figure 2. Ensemble response to two different odor inputs A and B. *Dots* depict the occurrence of an action potential. Large *arrows* on the right side indicate the odor focus for each odor. Note that the two ensemble responses differ only in the identities of the neurons that are synchronized in response to the odor input.

Since average firing rates, as well as average numbers of synchronous events, are independent of odor identity, ensemble responses differ only in the subset of neurons that fires synchronously within the ensemble. We used our wavelet-based metric to measure the similarity of the synchronization properties in two such ensemble responses. In these calculations, we varied both the distance between the odor foci (from 1 to 30 neurons apart) and the scale of the wavelet transform (from 0.5 to 300). As predicted, at very small scales, the wavelet transform discriminated between spike trains generated in response to very closely related odorants (distances of 1-3 between odor foci; Figure 3A), whereas at larger scales of the transform, closely-related odor responses were grouped together (Figure 3B).

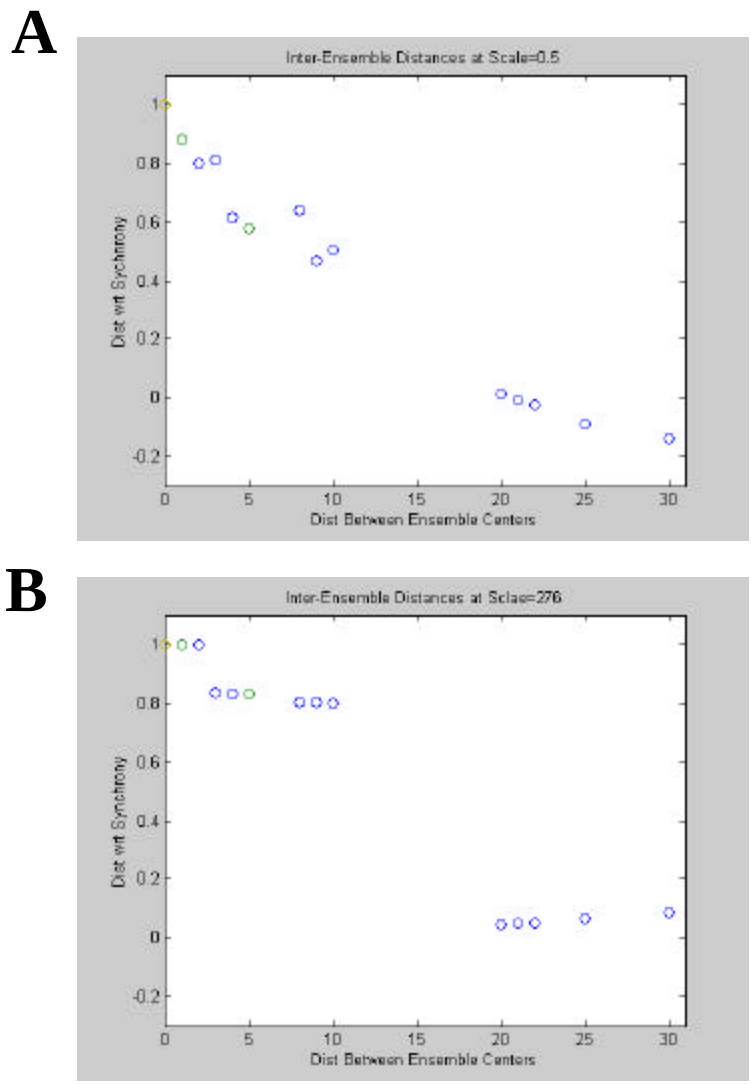

Figure 3: Correlations between multiple ensemble responses generated with different odor foci, calculated separately at two scale values. *Abscissa*, distances between odor foci. *Ordinate*, correlation values between the two ensembles. *A*, transform scale = 0.5. *B*, transform scale = 276.

References

Cleland TA, Linster C (2002) How synchronization properties among second order sensory neurons can mediate stimulus salience. *Behavioral Neuroscience* (in press).

Linster C, Cleland TA (2001) How spike synchronization among olfactory neurons can contribute to sensory discrimination. *J Comput Neurosc*i 10:187-193.

Song S, Miller KD, Abbott LF (2000) Competitive Hebbian learning through spike-timing-dependent synaptic plasticity. *Nat Neurosci* 3(9):919-26.