Directional statistics in spatiotemporal wave analysis

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Spatiotemporal wave activity in beta oscillations in motor cortex can be described in terms of the beta-band analytic LFP signal, which has both a magnitude and a phase, and who's real part is equal to the time-domain value of the beta-filtered signal.

$$z_k(t) = \beta_k(t) + i\,\mathrm{Hilbert}(\beta_k)(t) = r_k(t)e^{i\theta_k(t)}, \quad \text{where } k \text{ indexes over channels} \tag{1}$$

Circular statistics can be used to summarize the distribution of analytic signal phase, in order to detect synchrony and wave events. For example, Kuramoto's order parameter (Eqn. 2) summarizes phase concentration across the population. A related measure of synchrony (Eqn. 3) weights channels by their current amplitude. (In this document I use angle brackets $\langle\cdot\rangle$ to denote averaging over channels.) Note: the value in equation 2 is also more generally known as the first moment of circularly distributed data, sometimes denoted as R or R_1.

$$\text{Kuramoto} = \left\langle \frac{z}{|z|} \right\rangle \tag{2}$$

$$\text{Synchrony} = \frac{|\langle z\rangle|}{\langle |z| \rangle} \tag{3}$$

However, the evolution of the population of beta analytic LFP signals in phase space is complicated. There is dispersion in both amplitude and phase, and dispersion in amplitude can evolve into dispersion in phase and vice versa (e.g. Fig. 2). Directional statistics like (2) and (3) assess phase concentration, but fail to describe amplitude dispersion, or account for ways in which signal amplitude interacts with estimates of phase concentration.

A log-polar description of the analytic signal.

The analytic signal can be broken down into phase and magnitude components. The phase distribution can be described by circular statistics. The complex logarithm of the analytic signal separates phase and log-amplitude components (phase is identified modulo 2π).

$$\ln(z) = \ln(|z|) + i\arg(z) = r + i\theta \tag{4}$$

We model the log-amplitude as Gaussian.

$$\ln|z| \sim \mathcal{N}(\mu_r, \sigma_r) \tag{5}$$

The mean of a circular variable can be estimated as the angle of the average analytic signal vector (Eqn. 6). The circular standard deviation, which is analogous to the standard deviation of the circularly wrapped

Gaussian distribution, is defined in terms of a phase concentration measure S_z by equation 7. Phase concentration S_z is typically computed as the magnitude of the average of unit-length vectors, i.e. $\langle z/|z|\rangle$ as in equation 2. For our data, it is more reliable to perform a weighted average when computing S_z, since signal values with lower amplitude have poorly estimated phase, in which case S_z is analogous to the synchrony measure defined in equation 3.

$$\mu_\theta = \arg(\langle z\rangle) \tag{6}$$

$$\sigma_\theta = \sqrt{-2\ln(S_z)}, \quad S_z = \frac{|\langle z\rangle|}{\langle |z|\rangle} \tag{7}$$

The log-polar description of the analytic signal describes the dispersion in amplitude and phase separately, and is particularly appropriate for traveling wave states, which display uniformly high amplitude and a gradient of phases across the population (Fig. 2c). The log-polar model breaks down when the population is highly asynchronous with a mean signal value close to zero (Fig. 2e), when there amplitude and phase are interdependent (Fig. 2b,d), and when the phase distribution is bimodal (e.g. standing waves) (Fig. 2d).

Extending the log-polar description with a covariance term Kempter et al. (2012) devise a method of computing the correlation coefficient between a circular and linear variable. Their work was aimed at correlating the phase at which a spike occurs relative to hippocampal theta oscillations with a linear positional behavioral covariate. The approach is general, and will provide a way to compute a covariance term between log-amplitude and phase, extending the log-polar description to incorporate amplitude-phase dependence. However, the this does not resolve the problem of undefined phases when the signal is distributed about zero, and it does not resolve the problem of describing bimodally distributed phase.

The complex Gaussian model of the analytic signal.

The distribution of the beta analytic signal over channels can be approximated as a 2D Gaussian in the complex plane with a mean signal $\mu_z = \langle z\rangle$ and a covariance matrix Σ_z. This model has the advantage of capturing correlations between amplitude and phase (Fig. 2b). The distribution is well defined during asynchronous states, where the analytic signal is approximately normally distributed about the origin (Fig. 2e). The complex Gaussian distribution can handle those times in our data when the phase distribution is bimodal (Fig. 2d). Evolution of wave dynamics from asyncrony, to synchrony and standing waves, to traveling waves, can be captured by the complex Gaussian model when phase is not too disperse.

A polar model with negative amplitudes

Two of the conditions under which the log-polar statistics break down both occur when the distribution of analytic signal amplitudes includes zero. In the case when amplitude is distributed about 0, the rectification when computing $|z|$ leads to an inaccurate description of the data. In the case of standing waves, phase is concentrated, but the amplitude distribution crosses zero. This creates an apparently bimodal phase distribution, but the data would be better described as having a single preferred phase axis, with some channels having negative amplitude to explain the π phase shift.

Squaring the analytic signal will fold over negative amplitude values and eliminate "bimodal" phase distributions where the two modes are separated by π. This allows us to estimate the axis of phase concentration ϕ.

$$\phi = \frac{1}{2}\arg\langle z^2\rangle \tag{8}$$

We will represent out signal in polar (not log-polar) coordinates, inverting the sign of amplitude along the axis of phase concentration.

$$r = |z| \cdot \text{sign}[\cos(\arg(z) - \phi)], \quad \theta = \arg(z) + \begin{cases} \pi & \text{if sign}[\cos(\arg(z) - \phi] = -1 \\ 0 & \text{otherwise} \end{cases} \tag{9}$$

Figure 3 demonstrates that, while this model can describe synchronous events (Fig. 3a), and also can model situations with bimodal phase (Fig. 3b), it performs poorly overall. Identifying the axis of phase concentration can lead to unexpected (Fig. 3d) results. Times when the distribution of the signal is centered around 0 are poorly described (3c). Nevertheless, statistics from this model can be used to differentiate distributions with certain properties, and combined with the complex Gaussian and log-polar models, it may be useful in describing the data.

1 Concluding notes

Of the distributions explored so far, the complex Gaussian distribution most accurately describes the analytic signal distributions in our data. Times when the complex Gaussian approximation fails can be detected. For the purposes of characterizing synchrony, it may be enough to analyze statistics from both the the log-polar distribution and the complex Gaussian distribution.

Cited

1. Kempter, Richard, Christian Leibold, György Buzsáki, Kamran Diba, and Robert Schmidt. "Quantifying circular–linear associations: hippocampal phase precession." Journal of neuroscience methods 207, no. 1 (2012): 113-124.

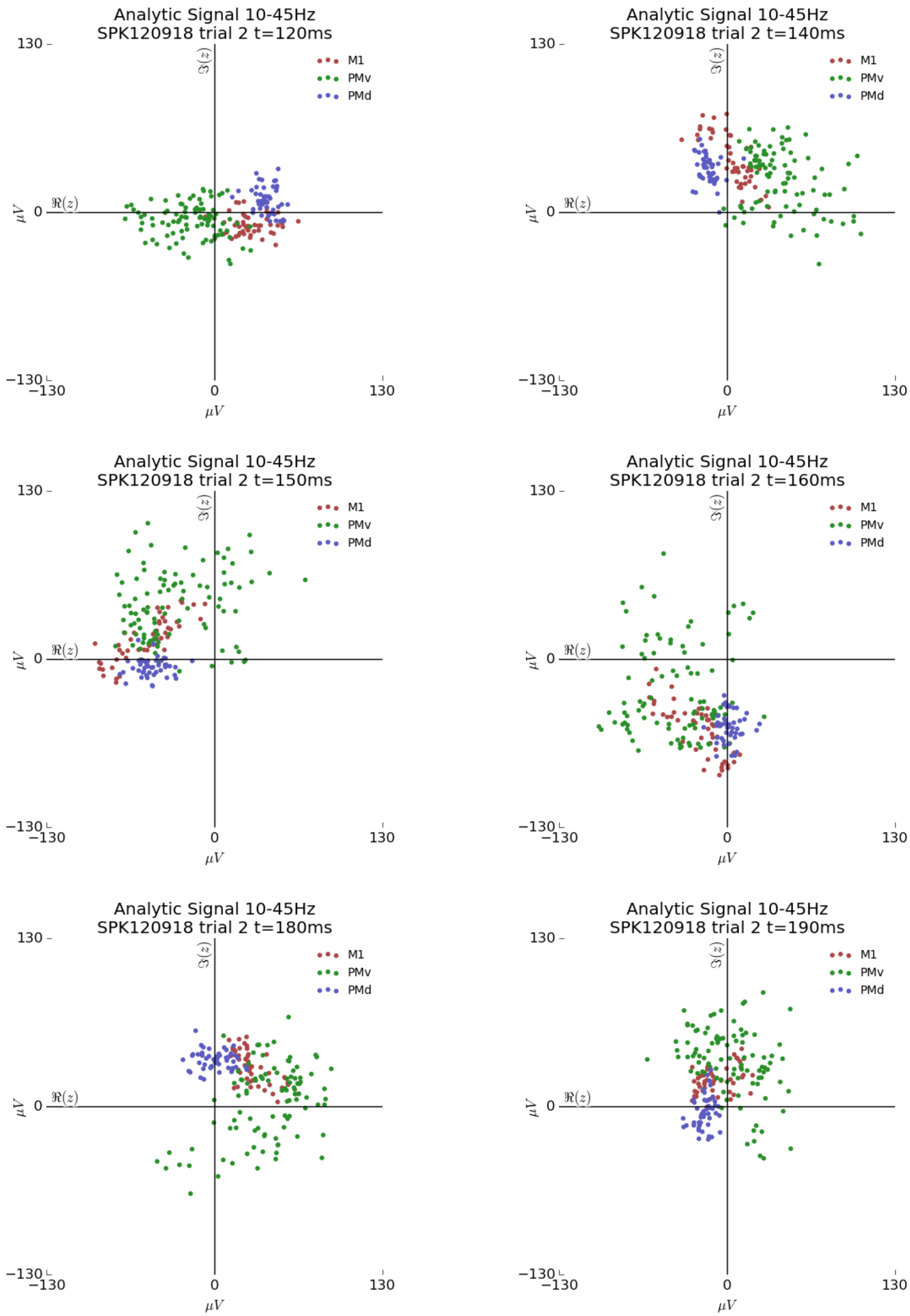
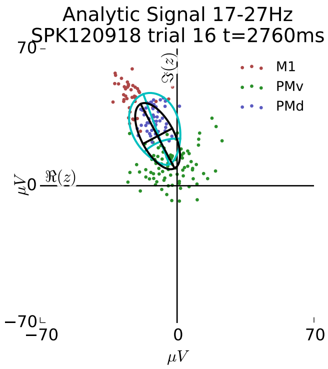
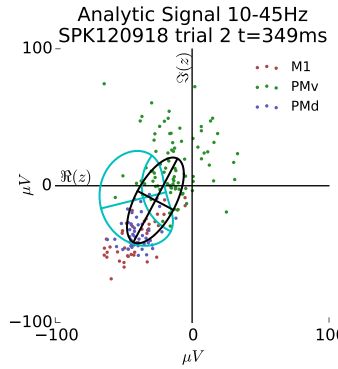


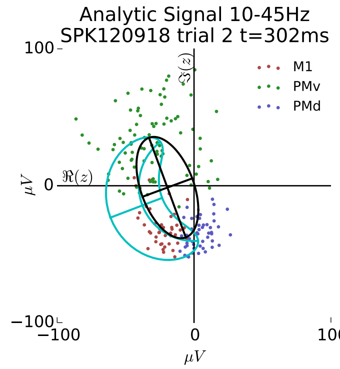
Figure 1: *Evolution of a wave event in analytic signal phase space* A wave event begins by excitation of oscillations in each channel. This excitation of amplitudes shifts, creating a plane wave where, in this case, the phase of area PM lags behind that in areas PMd and M1. This even lasts only for a few cycles of the beta oscillation, before collapsing back to an asynchronous state.



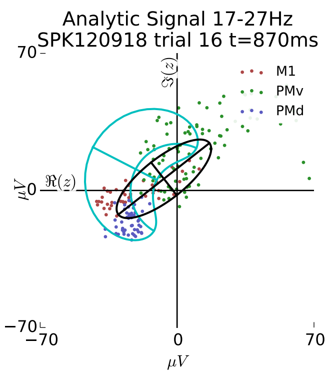
(a) Concentrated phase



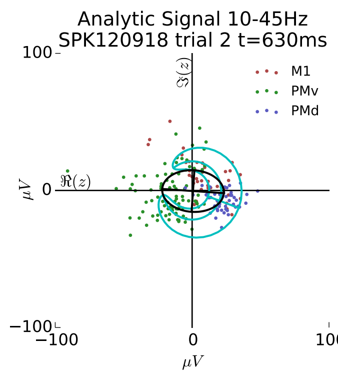
(b) Correlated amplitude and phase



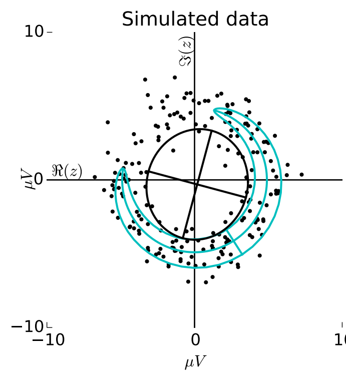
(c) Concentrated amplitude, disperse phase



(d) Bimodal phase concentration

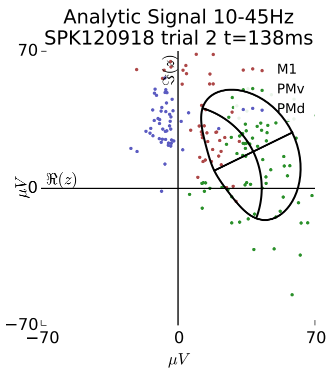


(e) Distribution about 0

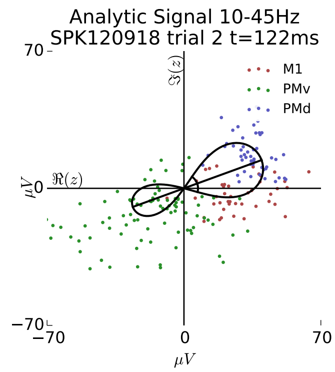


(f) Uniform phase

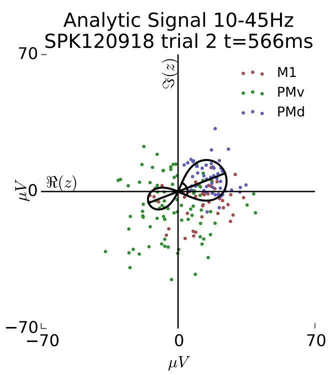
Figure 2: *Neither the complex Gaussian nor log-polar statistics perfectly describe the distributions of analytic signal.* In these plots, the black ellipse represents a complex Gaussian model of the data, with the ellipse boundary at one standard deviation, and the ellipse axes representing the eigenvectors of the covariance matrix Σ. The cyan contours represent a log-polar model of the data, which uses the mean and standard deviation of the log-amplitude, as well as the circular mean and standard deviation of the phases, to model the data in log-polar space. **(a)** When phase is concentrated, and not correlated with amplitude, both the log-polar statistics and the complex Gaussian distribution describe the data well. **(b)** When phase and amplitude are correlated, the log-polar model cannot capture the phase-amplitude dependence. **(c)** During traveling wave events, signal amplitude is high, and there is dispersion in phase. In these cases, the log-polar statistics are more appropriate than the complex Gaussian. **(d)** Traveling wave events appear to often evolve from states that show a mixture of synchrony and standing wave dynamics. The log-polar statistics break down when the phase distribution is bimodal, but the complex Gaussian can describe these states well. **(e)** At low signal amplitudes, the system is often asynchronous, and the phase and amplitude of the log-polar model are poorly defined. **(f)** Although rare or absent in our data, a hypothetical distribution with uniform phase and concentrated amplitude could occur, say, during traveling wave events with short wavelength. In this case, the complex Gaussian model is especially bad.



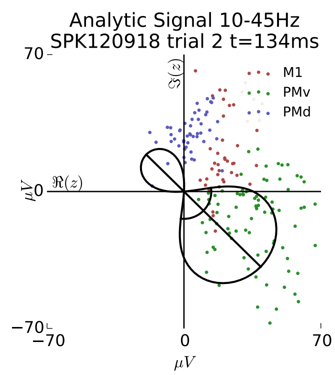
(a) Concentrated amplitude



(b) Correlated amplitude and phase



(c) Bimodal phase concentration



(d) Distribution about 0

Figure 3: *A polar model that allows negative amplitudes can capture distributions with bimodal phase.* These plots illustrate a polar model which first identifies an axis of phase concentration, and then restricts phase to within $\pi/2$ of the preferred phase axis, using negative amplitudes to represent signals that are close to π out of phase with the main axis phase concentration. **(a)** The negative-amplitude polar description accurately describes distributions with a clear amplitude and phase concentration **(b)** When the phase distribution is bimodal, this model captures that, albeit with a singularity at zero amplitude **(c)** When the distribution is centered at zero, this model attempts to approximate it as a distribution with bimodal phase. This is incorrect. **(d)** When there are dependencies between amplitude and phase, this model behaves strangely. In this case, the amplitude distribution does not truly cross zero, but the phases of the oscillations are dispersed enough that identifying the axis of phase concentration fails. This model cannot gracefully describe certain transitions from standing waves to plane waves.