TURN, TURN, TURN: TIME FOR PEACE. IT'S NOT TOO LATE! TEMPORAL PROCESSING IS BETTER MEASURED IN TERMS OF PHASE RATHER THAN LATENCY

A.B. Saul, *Dept Ophthalmology, Med. Col. of Georgia, Augusta, GA, USA*

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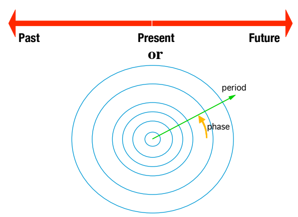
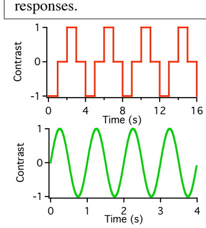
The topic: How does the brain think of time?



More practically, what's the best way to think of time when planning and analyzing experiments?

The methods: Data were collected from single neurons in cat and monkey LGN and V1. Extracellular recordings were made from anesthetized animals. Stimuli included temporally modulated stationary spots, and sparse or dense noise. Temporal modulations (see illustrations below) used were a 4-part stepping stimulus with a 4s cycle, and sinusoidal modulation at frequencies ranging from 0.125 to 32 Hz. Half-rise latencies were computed for each 16s trial. Phase statistics were computed from 4 or 8s trials, weighted by amplitudes.
Noise stimuli used 16-32 bars flashed bright, dark, or at background luminance.
Responses to noise stimuli were correlated with the stimulus to derive spatiotemporal receptive field maps. Singular value decomposition yielded spatiotemporally separable components. The resultant temporal waveforms will be called impulse responses.



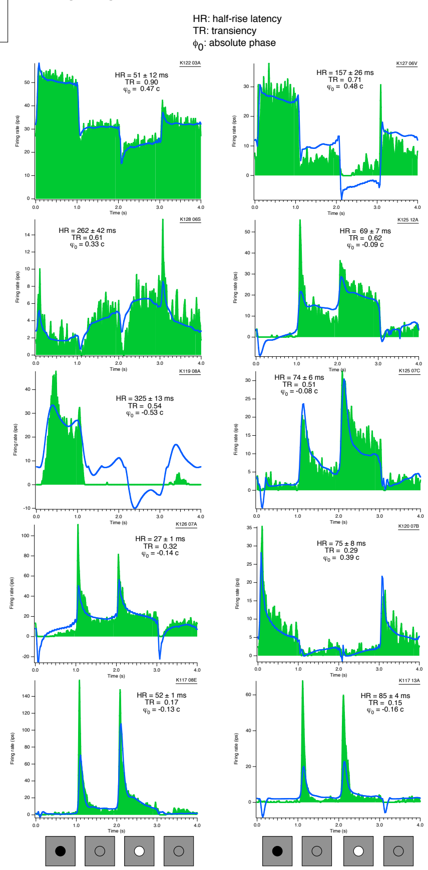
Temporal modulations: Stepping and sinusoidal

The message: Measurements in the time domain typically rely on few points from responses that are extended in time. For instance, latency is measured from one point to another. Most points in the response are ignored.
In contrast, phase measurements take into account the entire time course of the response.

Measuring timing for flashed stimuli

The examples show responses of kitten LGN cells to a flashing spot (green histograms). Half-rise latencies do take into account the response starting 100ms before spot onset up to the peak response, but the final measure refers only to the point halfway to the peak. Transiency is the ratio of the average response to the peak response. It is a minimal description of how sustained or transient the whole response might be.
Responses were also measured to the same spot modulated sinusoidally in time at a series of temporal frequencies. From the amplitude and especially from the phase data, predictions of the responses to the flashing stimulus were computed. The key parameter is absolute phase. These predictions capture details of the responses not captured by latency and transiency.

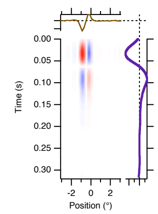
Details of the predictions: timing was linear, but amplitude was transformed by a function k0+k1*pred*|k3+pred|^{k2}.



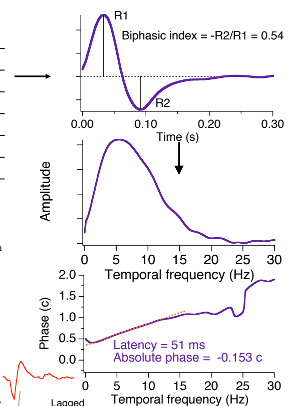
Analyzing impulse responses

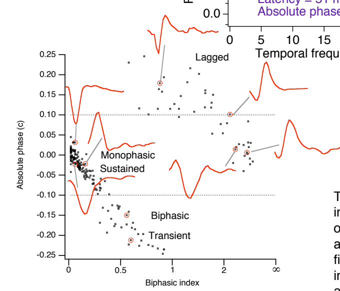
Impulse response functions have been analyzed in the time domain by calculating the ratio between the first 2 peaks, called the biphasic index. A biphasic index near 0 corresponds to a single dominant peak, a monophasic or sustained response. A biphasic index approaching 1 corresponds to nearly equal peaks, a biphasic, transient response.

Transforming the impulse response permits derivation of phase-based measures of timing. Absolute phase relates closely to the biphasic index as illustrated below. Small and large biphasic indices correspond to absolute phase values near 0. Biphasic indices near 1 correspond to absolute phase values near ±0.25c. Both of these measures are cyclic, but biphasic index ranges from 0 to ∞, which are the same point. The cyclic nature of absolute phase is more obvious.

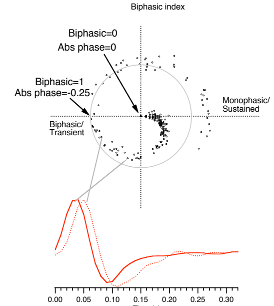


Receptive field map from a neuron in layer 4Cα of V1 in an anesthetized monkey





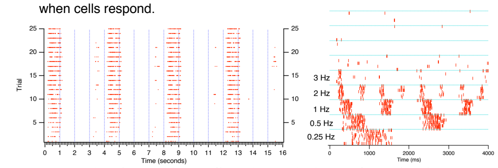
The biphasic index is insensitive to the shape of the impulse response aside from the sizes of its first 2 peaks. Triphasic impulse responses occur, and the widths and timings of the peaks can vary. By taking into account the entire time course, absolute phase captures more of the structure.



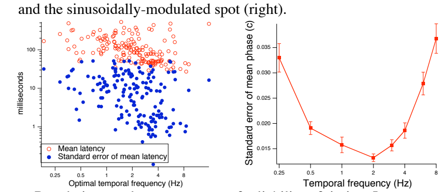
Shorter latencies don't necessarily correspond to more transient responses. Biphasic area only gives limited improvements over biphasic index.

Reliability of timing

Latency becomes a reliable measure at high temporal frequencies, but is inappropriate at low frequencies, where, by any definition, latency will be unreliable. However, timing is extremely reliable at low temporal frequencies when measured right. Phase values vary little across trials when cells respond.

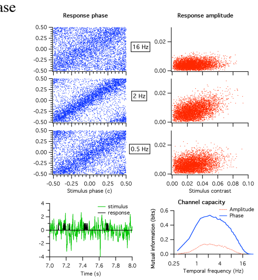


Raster plots from a kitten LGN cell tested with the 4-part flashing spot (left) and the sinusoidally-modulated spot (right).



Population results on measures of reliability of timing. Latency (red circles) tends to be lowest in cells with higher preferred frequencies. To a greater extent, the variance of latency (blue) is only small for cells tuned to high frequencies. In contrast, phase (right) is reliable at all frequencies for the same population.

Investigators commonly treat response amplitudes as if they contain the key information that characterizes cells. I have argued that timing is independent of amplitude, and that response phase is the key to understanding timing. Comparing these quantities is a problem that might be resolved by information-theoretic measures. The channel capacity of a model LGN cell is lower for amplitude than for phase



Conclusions: The world moves slowly. We need to move with it, including measuring how the world turns. Stimuli and responses are extended in time. When measurements only take into account a few points in time, they miss the richness of timing. On the other hand, simple quantities derived from phase vs. temporal frequency experiments account for much of temporal behavior. Timing is highly reliable at low temporal frequencies, as expected from our need to process time's slow ways. Patience is everything.