# Predictive Coding and Neural Communication Delays Produce Alpha-band Oscillatory Impulse Response Functions

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**Abstract:**

**Alpha (8-12Hz) oscillations are ubiquitous in the human brain. For example, the cross-correlation between temporally modulated white-noise visual stimuli and corresponding EEG waveforms reveals an impulse-response function (IRF) that reverberates at alpha frequency for several cycles. Yet the exact functional role of alpha rhythms in visual perception is still unknown. Here, I show that in a simplified model of visual cortex where neurons at one level seek to "explain away" the neuronal activation pattern at the previous level (i.e. "predictive coding"), alpha-band oscillatory IRFs naturally arise when neural communication delays between the two levels are taken into account. In fact, alpha oscillations are most robust when neuronal time constants and inter-areal delays are chosen with biologically plausible values –around 15-25ms and 10-15ms, respectively. The pervasive correlation between alpha rhythms and visual perception reported in numerous experimental studies could thus represent, in part, the signature of a basic computational principle: predictive coding.**

**Keywords: alpha rhythm; oscillations; predictive coding; neural delays; time constants; impulse-response function; EEG**

## Introduction

The relationship between alpha brain rhythms and visual perception is debated. Alpha is generally strongest in the absence of visual inputs, or when visual inputs are actively ignored –hence a proposed inhibitory role for alpha rhythms. On the other hand, alpha oscillations can also be positively correlated with visual inputs. For example, we recently reported strong and long-lasting alpha-band oscillations in the visual Impulse Response Function (IRF; VanRullen & Macdonald, 2012). The IRF is computed by cross-correlating occipital EEG signals recorded from human subjects watching a dynamic sequence of random (white noise) luminance values with the corresponding stimulus sequence (Figure 1). The existence of significant input-output correlations at lags of nearly 1s is surprising, given the typical neural time constants (<50ms) and the short-lived nature of visual-evoked responses (<0.5s); this could indicate a role for alpha rhythms in the maintenance of sensory information over time. Here, I investigate the presence of alpha-band oscillations in the IRF of a simple model of visual cortex that does not explicitly integrate or maintain information over extended periods, but merely tries to predict what comes next based on what was just there (predictive coding). The key insight is that typical neural communication delays between cortical areas can give rise to a reverberation of visual inputs at alpha frequency, as observed experimentally.

## Methods

The model used here is inspired by the classic predictive coding model of Rao & Ballard (1999), where each layer attempts to "explain away" (via inhibitory feedback) the activity pattern in the previous layer, which only communicates the "unpredicted" residual signals (via feedforward excitation). Since in our case the stimuli are strictly temporal luminance sequences, without any meaningful spatial arrangement (Figure 1), the model can be simplified greatly by ignoring spatial selectivity and considering a single neuron in each of two connected layers (corresponding, e.g. to LGN and V1 of the primate brain). The resulting circuit is illustrated in Figure 2. The specificity of the present approach is to consider the effects of the communication delay $\Delta T$ between the two layers (assumed here to be symmetric, for simplicity).

The neuron in layer 1 encodes the residual between the input sequence and the "prediction" received (with a delay $\Delta T$) from layer 2:
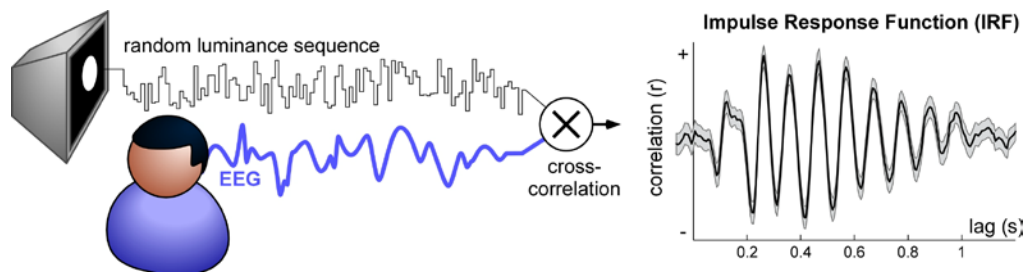


Figure 1. The IRF of the visual system can be derived by recording EEG while an observer watches a dynamic sequence of random (white noise) luminance values, then cross-correlating the two signals. The resulting IRF (right, typical subject, occipital electrode) displays strong and long-lasting alpha oscillations: visual inputs "reverberate" in the brain at ~10Hz.
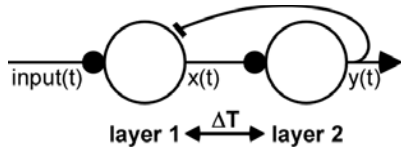
Figure 2. A simple predictive coding circuit: layer 1 receives sensory inputs; layer 2 aims to "explain away" activity in layer 1, which only sends the (unexplained) residuals. Filled circles and bars denote excitatory and inhibitory synapses, respectively. We investigate the influence of parameter ΔT, the (symmetric) communication delay between layers.

$$x(t) = input(t) - \lambda \cdot y(t-\Delta T) \qquad (1)$$

Here, $\lambda$ is a parameter that could be used to control the amount of feedback/predictive coding; in all present simulations it was fixed to $\lambda=1$.

The instantaneous response $y(t)$ of the neuron in layer 2 is governed by the differential equation:

$$dy/dt = x(t-\Delta T)/\tau - y(t)/\tau_{decay} \qquad (2)$$

where the first term is the integration of inputs from layer 1 (with a delay ΔT) and the second is a decay term ensuring that neurons return to their resting state in the absence of inputs. The temporal dynamics of neuronal integration and decay are governed by two time constants, respectively $\tau$ and $\tau_{decay}$, the latter of which was fixed to $\tau_{decay}=200ms$. Equation (2) was solved numerically with Euler's method and a 1ms time step.

For each pair of parameters $\tau$ and ΔT, the model was presented with 200 different white noise luminance sequences of 3s. The model's IRF was computed by cross-correlating each luminance sequence input(t) with layer 2's output y(t), and averaging the result over the 200 trials. That is, I assumed here that layer 2's activity is an approximation of the EEG signal (similar results were found, however, using layer 1's activity instead). The peak power and corresponding peak frequency of the IRF were finally extracted via FFT.
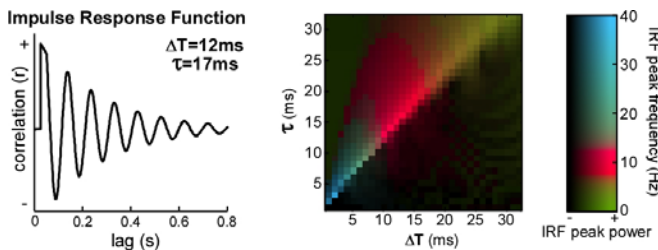


Figure 3. The IRF (left) obtained by cross-correlating the modeled "brain activity" y(t) and visual stream input(t) displays a strong alpha-band oscillation for parameters chosen with biologically plausible values (inter-areal communication delay ΔT=12ms, neural time constant τ=17ms). Systematic exploration of these two parameters (right) suggests that alpha reverberation is a robust phenomenon (red colors) within this biologically plausible range.

## Results

The results of a systematic exploration of parameter space are shown in Figure 3 (right). Several combinations of parameters give rise to oscillatory IRFs (brighter colors). Among these, IRF oscillations in the alpha (8-12Hz) frequency range are the most frequent (red colors). In particular, alpha-band IRF oscillations systematically arise when $\tau$ and ΔT lie in their "biologically plausible" range of respectively 15-25ms (Koch, Rapp & Segev, 1996) and 10-15ms (Shimegi et al, 2014). An example IRF obtained for $\tau=17ms$ and ΔT=12ms is shown in Figure 3 left.

## Discussion and Conclusion

While IRFs measured experimentally in response to white noise inputs can display long-lasting alpha reverberations, other electrophysiological responses (such as ERPs, event-related potentials) typically do not. The $\lambda$ parameter governing the strength of feedback communication (Equation 1) is likely to play a role here, as explored also by Heeger (2017): predictive coding might rely most strongly on feedback signals in situations where sensory inputs are most unpredictable (e.g. white noise).

In summary, long-lasting (~1s) alpha-band oscillatory reverberation of visual inputs, compatible with experimental observations, can be measured in a simple model with only short-term dynamics—each neuron only integrates information over ~20ms (neural time constant $\tau$), and the delays for information transmission (ΔT) are also restricted to <20ms. This implies that the ubiquitous alpha rhythm could reflect, in part, the computations involved in predictive coding. Future work could extend the model to inputs that are organized spatially as well as temporally, and consider the pattern of spatial selectivity (i.e., the connection weights) across multiple neurons in each layer.

## Acknowledgments

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