

# Computational Modeling of Traveling Waves Using MEG-EEG in Human

**Laetitia Grabot (laetitia.grabot@u-paris.fr)**

Université Paris Cité, CNRS, Integrative Neuroscience and Cognition Center  
F-75006 Paris, France

**Garance Merholz (gmerholz@gmail.com)**

Université Paris Cité, CNRS, Integrative Neuroscience and Cognition Center  
F-75006 Paris, France

**Jonathan Winawer (jonathan.winawer@nyu.edu)**

Department of Psychology, New York University  
New York, NY 10003, United States  
Center for Neural Science, New York University  
New York, NY 10003, United States

**David J. Heeger (david.heeger@nyu.edu)**

Department of Psychology, New York University  
New York, NY 10003, United States  
Center for Neural Science, New York University  
New York, NY 10003, United States

**Laura Dugué (laura.dugue@u-paris.fr)**

Université Paris Cité, CNRS, Integrative Neuroscience and Cognition Center  
F-75006 Paris, France  
Institut Universitaire de France (IUF)  
Paris, France



## Abstract

Recent studies suggest that brain oscillations are traveling waves in cortex. Yet, studying oscillations propagating within single cortical areas has so far been restricted by the need for invasive measurements. Non-invasive techniques such as MEG or EEG are limited by technical and biophysical constraints (e.g., source summation, volume conduction, low signal-to-noise ratios). To overcome these issues, we developed a novel model-based neuroimaging approach. (1) The putative neural sources of a propagating oscillation were modeled within the primary visual region (V1) via retinotopic mapping from functional MRI recordings (encoding model); and (2) the modeled sources were projected onto the M-EEG sensor space to predict the resulting signal (forward biophysical head model). We tested our model by comparing its predictions against the M-EEG signal obtained when participants viewed visual stimuli designed to elicit either fovea-to-periphery or periphery-to-fovea traveling waves, or standing waves in V1. Correlations on pairwise sensor relationships between predicted and measured data revealed good model performance. Crucially, the model was able to distinguish M-EEG recordings while participants viewed traveling stimuli in one direction compared to the opposite direction. Our model aims at recovering the spatio-temporal dynamics of cerebral activity from non-invasive measurements to better apprehend the neurophysiological bases of cognition.

**Keywords:** cortical oscillations; traveling waves; M-EEG; forward model; encoding model; model-based neuroimaging

Brain activity is typically studied by reducing its dimensionality along either the spatial (e.g., spatial networks from fMRI) or the temporal dimension (e.g., cortical oscillations in specific brain areas or sensors). The need for an integrated view of brain functioning across time and space was advocated to understand the multiscale basis of cognition (Kopell et al., 2014; Bassett & Sporns, 2017). One step to achieve such a goal is to consider brain oscillations as propagating across the cortex (Muller et al., 2018). Yet, the detection of traveling waves propagating locally, i.e., within a single brain area, was only studied using invasive techniques (V1: Chemla et al., 2019; V4: Zanos et al., 2015; M1: Takahashi et al., 2015) or indirectly via behavioral measures (Sokoliuk & VanRullen, 2016; Fakche & Dugué, 2022). Strong technical constraints limit the use of non-invasive techniques such as MEG or EEG to detect traveling waves in the human brain. We propose a new model-based neuroimaging approach circumventing these issues.

The classic approach in M-EEG consists in inferring source activity (typically, cerebral cortex) from sensor data. This inverse problem is mathematically ill-posed because there are many more possible sources than sensors. Our approach differs by employing an encoding model (Kupers, Benson, Winawer, 2021). Specifically, the model has two steps: stimulus to sources and then sources to sensors. The stimulus-to-

source prediction is a traveling wave in V1, constrained by spatial and temporal properties of the stimulus, in combination with fMRI-derived retinotopic maps. The source-to-sensor prediction is derived from a biophysical head model. Measured data are then compared to these predicted sensor data to characterize the cortical dynamics.

The long-term goal of the model is to use it to infer whether stimuli that do not contain traveling waves nonetheless induce traveling waves in cortex. Here, to validate the model, we presented dynamic visual stimuli to participants while simultaneously recording MEG and EEG. The stimuli were designed to induce either standing or traveling waves in retinotopic area V1. We expected to identify the induced patterns using our modeling method.

## Material & Methods

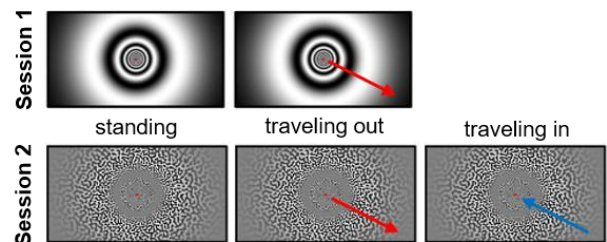
**M-EEG and MRI data acquisition.** 28 participants took part to the study, approved by the Ethics Committee on Human Research (# 2017-A02787-46). All performed a first M-EEG session and an MRI session (anatomy and retinotopic mapping). 19 performed an additional M-EEG session. In the first M-EEG session, participants fixated a dot at the center of the screen (Fig 1), while the luminance of the screen was modulated according to equation (1) or (2) (traveling out, from fovea to periphery, and standing condition, respectively). A trial lasted 2 seconds (160 trials total per condition).

$$(1) \text{trav}(x,t) = A \sin(2\pi F_s x - 2\pi F_t t + \varphi) + c$$

$$(2) \text{stand}(x,t) = A \sin(2\pi F_s x) \cdot \cos(2\pi F_t t + \varphi) + c$$

with  $x$ , the radial distance of a given pixel on the screen, after correction for cortical magnification,  $A = 0.5$ ,  $c = 0.5$ ,  $F_t = 5$  Hz,  $\varphi = \pi/2$ ,  $F_s = 0.05$  cycles/mm of cortex.

In the second M-EEG session, we added a static carrier to the luminance modulator to increase V1 responsiveness. The carrier was Gaussian white noise with a spatial frequency tuned to V1's preferred spatial frequency (Broderick, Simoncelli, Winawer, 2022). Three conditions were tested to elicit standing and traveling waves in opposite directions, from fovea to periphery and vice versa, in V1 (standing, traveling out and traveling in conditions, respectively; Fig 1).



**Figure 1.** Visual stimuli designed to elicit standing or traveling waves (in two opposite directions) in V1.

**Computational model.** The first part simulates brain oscillations that propagate in V1. Using the retinotopy-derived eccentricity map (Benson & Winawer, 2018), we mapped the spatio-temporal dynamics of the stimuli onto the cortical surface. The second part (forward model) estimates the signals produced at the M-EEG sensors from simulated V1 activity.

**Comparison between predicted and measured data.**

To quantify the model's predictive power, we compared between-sensor phase and amplitude between predicted and measured data. To do so, we extracted the instantaneous 5Hz-phase and amplitude of the evoked time series using time-frequency decomposition with Morlet wavelets. For a given pair of sensors, we calculated the amplitude ratio and phase difference between sensors. We then combined the obtained amplitude and phase in a complex number. This was done for every pair of sensors, for measured and predicted signals independently, which we then compared using Pearson correlation.

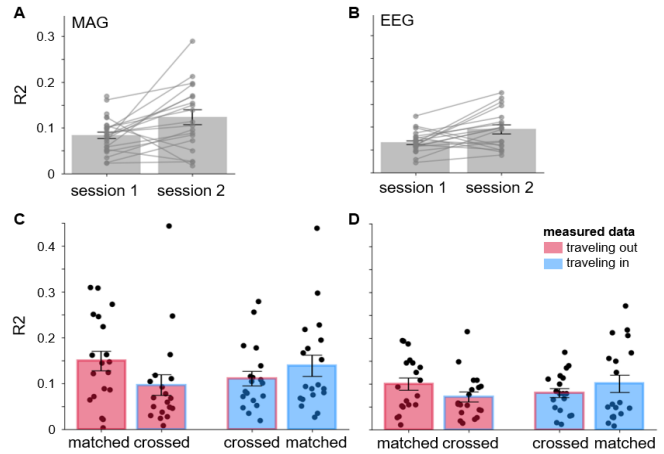
**Results & Discussion**

To quantify how much the model predicts the measured data, we compared the between-sensor relationships (phase and amplitude) between predicted and measured data for each condition. The correlation coefficients calculated per session and sensor type were statistically significant for most participants (MEG magnetometers, MAG: 26/28 in session 1, 17/19 in session 2, Fig 2A; EEG: 22/28 in session 1, 17/19 in session 2, Fig 2B; MEG gradiometers, GRAD: 22/28 in session 1, 17/19 in session 2), suggesting that the model does capture part of the between-sensor relationships in measured data.

Next, to test the specificity of the model, we compared the measured data from the traveling condition to the predicted data of the standing condition, and vice versa. We expected that the matched comparison (i.e., standing model to standing data and traveling model to traveling data) explains more variance than the crossed comparison (standing model to traveling data and traveling model to standing data). We found 3 key results:

**(1) Adding the static carrier to the stimulus boosted the model performance.** We ran a linear mixed model on the correlation coefficients with sessions, comparison (matched/crossed), measured data (traveling/standing) and sensor type (MAG, GRAD, EEG) as predictors, and participants as random effect. We found a main effect of session ( $F = 5.82, p = 0.027$ ) and sensor type ( $F = 6.38, p = 0.004$ ), indicating that the correlation coefficients were stronger in session 2 (Fig 1A) and in MAG compared to GRAD (post-hoc t-test,  $t(18) = 5.06, p = 8.1e-5$ ; other tests: n.s.). A post-hoc analysis showed that adding the static carrier

boosted the model performance by increasing the strength of the neural signal (data not shown).



**Figure 2:** Correlation coefficients on between-sensor relationships between measured and predicted data. Correlation for both traveling and standing conditions, for each session and channel type (A: MAG, B: EEG). To test the model specificity, both predicted data from traveling out and in models (red and blue outlines, resp.) are compared to the measures from the matching condition (red and blue for traveling out and in, resp.; session 1: C; session 2: D). Black dots: participants. Error bar: standard error of the mean.

**(2) The traveling model better explained both the traveling and standing measured data.** Specifically, we found no effect of comparison ( $F = 3.588, p = 0.074$ ), but a significant interaction between comparison and measured data ( $F = 40.59, p = 5.32e-6$ ). A post-hoc hypothesis is that the default response of the visual system to any –traveling or standing– stimulus involves traveling waves.

**(3) The model was specific to the traveling wave direction.** Specifically, we compared the two stimuli traveling in opposite directions (out vs. in). We ran a linear mixed model with comparison (matched/crossed), measured data (traveling in/out) and sensor type (MAG/GRAD/EEG) as predictors, and participants as random effect. There was a main effect of comparison ( $F = 13.07, p = 0.002$ ) and no significant interactions. Thus, the correlation coefficients were stronger when the tested model matches the measured data (Fig 2). There was also a significant effect of sensor type ( $F = 1.34, p = 0.02$ ): correlation coefficients were stronger in MAG compared to GRAD (post-hoc t-test,  $t(18) = 4.00, p = 0.001$ ; other tests: n.s.).

In summary, the model is able to accurately determine the direction of traveling waves using non-invasive measures of brain activity. This represents a first proof-of-concept of a tool designed to investigate the spatio-temporal dynamics of the brain.

## Acknowledgments

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement N° 852139 to Laura Dugué). We thank Camille Lépingle for her help with data acquisition and preprocessing.

consistent with wave propagation in motor cortex. *Nature communications*, 6, 7169.

Zanos, T. P., Mineault, P. J., Nasiotis, K. T., Guitton, D., & Pack, C. C. (2015). A sensorimotor role for traveling waves in primate visual cortex. *Neuron*, 85(3), 615–627.

## References

Bassett, D. S., & Sporns, O. (2017). Network neuroscience. *Nature neuroscience*, 20(3), 353–364.

Benson, N. C., & Winawer, J. (2018). Bayesian analysis of retinotopic maps. *eLife*, 7, e40224.

Broderick, W. F., Simoncelli, E. P., & Winawer, J. (2022). Mapping spatial frequency preferences across human primary visual cortex. *Journal of vision*, 22(4), 3.

Chemla, S., Reynaud, A., di Volo, M., Zerlaut, Y., Perrinet, L., Destexhe, A., & Chavane, F. (2019). Suppressive Traveling Waves Shape Representations of Illusory Motion in Primary Visual Cortex of Awake Primate. *The Journal of neuroscience*, 39(22), 4282–4298.

Fakche, C., Dugué, L. (2022). Perceptual cycles travel across retinotopic space. *bioRxiv* 2022.05.04.490030;

Kopell, N. J., Gritton, H. J., Whittington, M. A., & Kramer, M. A. (2014). Beyond the connectome: the dynamo. *Neuron*, 83(6), 1319–1328.

Kupers, E. R., Benson, N. C., & Winawer, J. (2021). A visual encoding model links magnetoencephalography signals to neural synchrony in human cortex. *NeuroImage*, 245, 118655.

Muller, L., Chavane, F., Reynolds, J., & Sejnowski, T. J. (2018). Cortical travelling waves: mechanisms and computational principles. *Nature reviews. Neuroscience*, 19(5), 255–268.

Sokoliuk, R., & VanRullen, R. (2016). Global and local oscillatory entrainment of visual behavior across retinotopic space. *Scientific reports*, 6, 25132.

Takahashi, K., Kim, S., Coleman, T. P., Brown, K. A., Suminski, A. J., Best, M. D., & Hatsopoulos, N. G. (2015). Large-scale spatiotemporal spike patterning