Tracking time by simulating the sensory world

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Abstract

Theories of oscillatory tracking propose that neural oscillations model external temporal structure by phase-coupling to environmental rhythms. However, methodological challenges make evidence for these proposal sparce, particularly in the visual domain which has predominantly focused on how theta and alpha oscillations parse perception independently of external temporal structure. Using a new empirical approach we aimed to address this question. Participants attended rhythmic visual displays and we used rate-specific phase coherence MEG measures as well as multivariate decoding to investigate the cortical tracking of this temporal structure. We show rate-specific phase-coupling of motor regions to the tracked rhythm, specifically when timing is task-relevant. Crucially, this explicit tracking of temporal structure relies on temporally precise sensory predictions in visual areas that interestingly appear regardless of task instruction. We propose a mechanism by which automatic sensory simulation yields an information envelope that is read out by motor areas when required to derive temporal estimates. Under this view, temporal predictions are simply derivatives, and sensory predictions are their necessary bedrock.

Keywords: temporal predictions; oscillatory tracking; predictive processing;

Introduction

Relevant sensory information is often embedded within predictable temporal structure. Oscillatory tracking, a view largely popularized by speech and music research, suggests that sensory rhythms are tracked through phase-aligned neural oscillations (Lakatos et al., 2008; Obleser & Kayser, 2019). These consequently act as adaptive models of the world's temporal structure and can coordinate its processing.

Challenging this account have been difficulties in isolating oscillatory tracking signatures from evoked potentials that produce similar neural response profiles (van Bree et al., 2021). These especially need addressing in the visual domain where a focus on environment-independent perceptual rhythms in the theta and alpha range (Helfrich et al., 2018) has largely predominated research, at the expense of investigations into how the brain flexibly tracks visual rhythms in its environment.

As well as debates over the presence of oscillatory tracking, its function is unclear. Prominent theories implicate it in specifically supporting temporal processing which so far lacks empirical support (van Bree et al., 2021). Furthermore, predictive processing accounts suggest that the brain continuously predicts upcoming stimuli in a time-resolved manner (Kok et al., 2017). How the temporal information contained within sensory predictions relate to explicit temporal tracking is unknown.

Methods

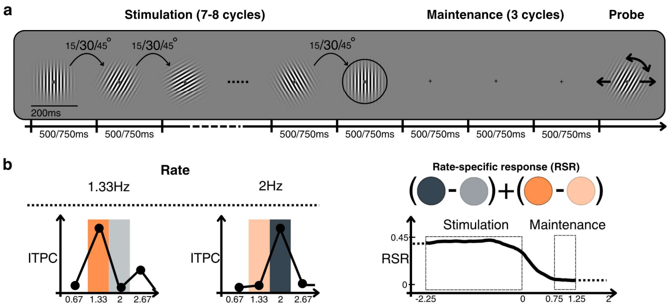

Figure 1: A) Trial design. B) Conceptual illustration of rate-specific inter-trial phase consistency (ITPC) analysis.

Design We conducted an MEG study in which participants attended rhythmic visual sequences of rotating Gabor patches (Figure 1A). Their onsets were separated by either 500 or 750ms and orientations changed with a trial-fixed step size in either the clockwise or counter-clockwise direction. Following the marked final Gabor of each sequence, a 'Maintenance' window started that lasted three cycles of the preceding stimulation frequency within which participants simply fixated without any visual stimuli. This window ended with the presentation of a probe that participants were asked to judge. In orientation blocks, participants judged whether the target showed the orientation that would have followed the final one of the sequence. In timing blocks, they judged whether it appeared at an 'on-beat' timepoint if the preceding rhythm had continued. On both dimensions and orthogonally to each other, targets were 'off' on 22% of trials. Stimuli were identical regardless of block, what differed was the judgement.

Rate-specific response (RSR) We used rate-specific inter-trial phase consistency (ITPC, Figure 1B) as a measure of oscillatory tracking, inspired by past work in the auditory domain (van Bree et al., 2021). We considered this measure separately in a 'Stimulation' window as the visual rhythm unfolded and in the Maintenance window between the rhythmic sequence and the probe to isolate oscillatory tracking signatures from evoked responses. In both windows, we compared RSR responses in the two tasks to each other and zero.

Sensory simulation analysis To investigate neural representations of predicted visual contents, we used an inverted encoding model (IEM) and focused on decoding evidence for the three inferred orientations that result from extrapolation of the rhythmic sequence into the Maintenance window (Figure 2A, B). We formalized predictions about their predicted activity profiles in signed difference matrices (SDMs, Figure 2C) and correlated these with matrices filled using participants' decoding output to assess their degree of sensory simulation.

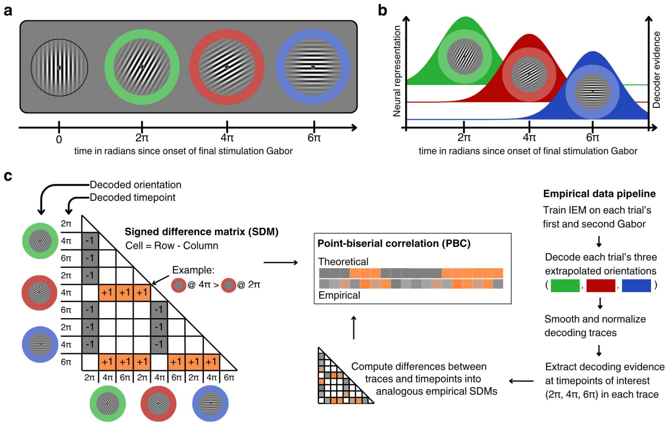

Figure 2: A) Example of temporally-specific orientation predictions for each of the Maintenance window's three 'empty' cycles. B) The timecourse of these predictions operationalised as IEM decoding evidence assuming sensory simulation. C) SDMs as models of sensory simulation are fit to participants' decoding output.

Results

Ongoing visual stimulation elicited a scalp-wide RSR response, expectedly maximal at occipital sensors and not different between tasks. More interestingly, in the Maintenance window, we found a significant RSR specifically in the timing task, localized to a cluster in motor areas (Figure 3A). The strength of this response furthermore predicted performance on the timing but not the orientation task (Figure 3B).

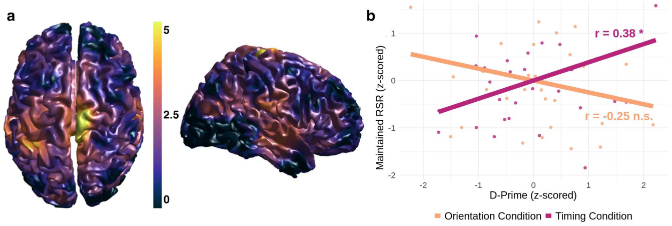

Figure 3: A) Timing-task Maintenance window RSR, source-localized t-values against 0. B) Correlation between task-specific activity from cluster in A) and behavioural performance.

However, decoding of predicted Gabor orientations showed that participants engaged in temporally and feature-specific sensory simulation across both tasks (Figure 4A). Importantly, the strength of sensory simulation scaled the strength of the maintained RSR in the timing task specifically (Figure 4B). Combined with the apparent automaticity of the sensory simulation response, this suggests that motor-based tracking responses may read out ongoing sensory simulation.

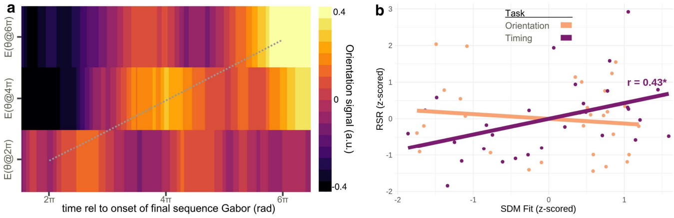

Figure 4: A) Task and participant-averaged decoding traces show evidence progressing in line with predicted orientation. B) Strength of sensory simulation predicts specifically timing task Maintenance RSR (Figure 3).

Discussion

The finding of motor-based tracking extends recent insights from audition into vision (Cannon & Patel, 2021; Morillon & Baillet, 2017). However, in contrast to dominant models positing motor regions in an orchestrating role for temporal predictions, our results show that temporal predictions are inherently embedded in the visual system's ongoing prediction of the sensory world. Abstracting over the specifically predicted stimuli, this provides a predicted information time course that motor regions simply 'read out' when explicit timing judgements are task-relevant.

Acknowledgments

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References

Cannon, J. J., & Patel, A. D. (2021). How Beat Perception Co-opts Motor Neurophysiology. *Trends Cogn Sci*, *25*(2), 137-150. https://doi.org/10.1016/j.tics.2020.11.002

Helfrich, R. F., Fiebelkorn, I. C., Szczepanski, S. M., Lin, J. J., Parvizi, J., Knight, R. T., & Kastner, S. (2018). Neural Mechanisms of Sustained Attention Are Rhythmic. *Neuron*, *99*(4), 854-865 e855. https://doi.org/10.1016/j.neuron.2018.07.032

Kok, P., Mostert, P., & de Lange, F. P. (2017). Prior expectations induce prestimulus sensory templates. *Proc Natl Acad Sci U S A*, *114*(39), 10473-10478. https://doi.org/10.1073/pnas.1705652114

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of Neuronal Oscillations as a Mechanism of Attentional Selection. *Science*, *320*. https://doi.org/10.1126/science.1154735

Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proc Natl Acad Sci U S A*, *114*(42), E8913-E8921. https://doi.org/10.1073/pnas.1705373114

Obleser, J., & Kayser, C. (2019). Neural Entrainment and Attentional Selection in the Listening Brain. *Trends Cogn Sci*, *23*(11), 913-926. https://doi.org/10.1016/j.tics.2019.08.004

van Bree, S., Sohoglu, E., Davis, M. H., & Zoefel, B. (2021). Sustained neural rhythms reveal endogenous oscillations supporting speech perception. *PLoS Biol*, *19*(2), e3001142. https://doi.org/10.1371/journal.pbio.3001142