

Oscillation or not—Why we can and need to know (commentary on Doelling and Assaneo, 2021)

Sander van Bree^{1,2}  | Andrea Alamia^{3,4}  | Benedikt Zoefel^{3,4} 

¹Centre for Cognitive Neuroimaging, Institute for Neuroscience and Psychology, University of Glasgow, Glasgow, UK

²Centre for Human Brain Health, University of Birmingham, Birmingham, UK

³Centre de Recherche Cerveau et Cognition, CNRS, Toulouse, France

⁴CerCo, Université Toulouse III Paul Sabatier, Toulouse, France

Correspondence

Sander van Bree, Centre for Cognitive Neuroimaging, Institute for Neuroscience and Psychology, University of Glasgow, Glasgow, UK.

Email: sandervanbree@gmail.com

Benedikt Zoefel, Université Toulouse III Paul Sabatier, Toulouse, France.

Email: benedikt.zoefel@cnrs.fr

Funding information

Centre National de la Recherche Scientifique; Agence Nationale de la Recherche

KEYWORDS: biophysics, brain dynamics, cognitive neuroscience, entrainment, neural oscillations

1 | INTRODUCTION

Neural oscillations have been the subject of intense research for nearly a century. They are a core phenomenon of the central nervous system (Llinás, 1988), and evidence for their involvement in cognitive processes has been mounting ever since their discovery (Ward, 2003).

Yet, identifying oscillations is not always easy. In the presence of a rhythmic stimulus, neural ensembles can show rhythmic behaviour even if they cannot be considered an oscillator—that is, they are unable to produce oscillatory activity on their own, but simply reflect the regularity of the stimulus. In various fields of research, such as that of “neural entrainment,” this has led to immense efforts to distinguish “true” neural oscillations from other neural processes that can produce remarkably similar responses in certain situations (Zoefel et al., 2018).

In a recent article, Doelling and Assaneo (2021) propose that the question “oscillation or not” hampers progress in these research fields. They argue that the

phenomenon “neural oscillation” comprises various heterogeneous neural processes; consequently, the line between oscillating and non-oscillating systems is blurred and therefore meaningless to draw.

Here, we argue against this conclusion and base our argumentation on one crucial notion: Despite their heterogeneity, neural oscillations are a separate class of neural processes. This is because neural oscillations have *unique* and *shared* properties. Unique properties are those that *only* oscillators have. Shared properties are those that *all* oscillators or all oscillators within a subclass have—for example, all oscillators with a specific frequency. Unique properties are the reason *we can know* whether oscillations are present, as they allow us to distinguish them from non-oscillatory processes. The existence of such properties therefore contradicts the notion that there is no clear line between oscillating and non-oscillating systems. Shared properties are the reason *why we need to know* whether oscillations are present, as, once a member of the “oscillation family” (or a subclass) is identified, it can be assumed to possess

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *European Journal of Neuroscience* published by Federation of European Neuroscience Societies and John Wiley & Sons Ltd.

such properties. Importantly, this means that an answer to the question “oscillation or not” advances certain research fields rather than impedes them, as it constrains the possible neural dynamics involved and allows us to make informed predictions on a variety of levels.

2 | HOW WE CAN KNOW: UNIQUE PROPERTIES

The following properties are unique to oscillators and therefore sufficient for their identification. Unique properties are not necessarily shared by all oscillators. In this case, the *absence* of such properties does not lead to the conclusion that no oscillator is involved.

- **Eigenfrequency:** All oscillators have a “natural” frequency, their eigenfrequency. This is the input frequency they respond to most strongly (Hutcheon & Yarom, 2000), or the frequency they oscillate at in the absence of external stimulation.
- **Arnold Tongue:** An external, rhythmic stimulus can synchronize a neural oscillator more readily if the stimulus rate is close to the oscillator’s eigenfrequency. The more distant the two (stimulus rate and neural eigenfrequency), the higher the stimulus intensity needs to be to reliably synchronize the oscillator. This leads to a characteristic triangular shape—an Arnold Tongue—when the degree of stimulus-brain synchronization is visualized as a function of rate and intensity of the external rhythm (relative to those of the neural oscillator; Pikovsky et al., 2003).
- **Convergence:** If sufficiently close to the eigenfrequency, a periodic force (i.e., an external stimulus) will alter the frequency and phase of an oscillator until they converge to a stable value (Fröhlich, 2015). The time (e.g., number of cycles) it takes to reach stability depends on the position in the Arnold Tongue (i.e., it varies as a function of rate and intensity of the rhythmic stimulus).
- **Independence:** Only oscillators show rhythmic behaviour in the absence of a rhythmic stimulus. This property comprises several scenarios: (1) rhythmic neural activity in the absence of any stimulus input (“spontaneous”); (2) rhythmic neural activity evoked (and “reset”) by non-rhythmic stimulus input (e.g., a pulse); (3) rhythmic neural activity which *outlasts* rhythmic stimulus input. How long such “echoes” last (or whether they are present at all) depends on the dampening of the oscillatory system.

3 | WHY WE NEED TO KNOW: SHARED PROPERTIES

Once the involvement of a neural oscillator in a given phenomenon is established (e.g., based on unique properties), then properties shared by all (or a subclass of) oscillators can be reliably associated with that phenomenon.

- **Neurophysiological properties.** Having an eigenfrequency is both unique to and shared by all oscillators. In addition, all neural oscillations reflect rhythmic changes in excitability (Buzsáki & Draguhn, 2004; Singer, 2018), produced by neuronal interactions that crucially rely on inhibition (Llinás, 1988). Oscillations stem from networks hard-wired to produce rhythmic activity on their own, at or close to their eigenfrequency. They therefore entail a component of activity that goes beyond a simple input–output relay of information and seems optimized for internal control of stimulus processing (see next point). Some properties are shared only by a subclass of oscillators, such as distinct neural architectures underlying different oscillatory frequencies (Womelsdorf et al., 2014). Knowing the eigenfrequency of an oscillator therefore provides us with valuable information about its neural origins and functional role.
- **Functional properties.** The functional role of a neural oscillator is fundamentally linked to its rhythmic variation in excitability. If these excitability cycles are synchronised between different neural populations, this leads to efficient neural communication (Fries, 2015). The oscillatory cycle is also a gatekeeper for external stimulation, rhythmically amplifying and attenuating input, a system that can ultimately serve attentional selection (Lakatos et al., 2008). Together, a common theme across neural oscillations is the role of gating, routing, and structuring of information. Identifying an oscillation indicates that such a role might be associated with the observed rhythmic brain activity.
- **Methodological properties.** Once the involvement of a neural oscillator has been established, methods developed to manipulate oscillations can be applied more efficiently. Such methods include transcranial alternating current stimulation (tACS), which has been shown to follow an Arnold Tongue (Huang et al., 2021) and produce rhythmic effects that outlast the electric stimulation (van Bree et al., 2021). Neural oscillations at specific frequencies can also be manipulated pharmacologically (Lozano-Soldevilla et al., 2014).

We illustrate our line of argumentation with an example. Recent research has shown that the rhythm of visual speech cues modulates the ability to detect an auditory target (Biau et al., 2021). This effect could merely reflect a passive relay of visual information to the auditory system and lead to a rhythmic modulation of auditory perception only because the information itself is rhythmic. The oscillatory effect, however, only appears after several cycles of visual stimulation, a property that speaks for the involvement of neural oscillations (*convergence* described above). This conclusion allows us to link the observed phenomenon with other properties oscillations possess. For example, it suggests that vision can control auditory sensitivity by modulating neural excitability, acting as a rhythmic gatekeeper for auditory information. It also predicts that we can use tACS to alter cross-modal perception, but only when we successfully identify and target the eigenfrequency of the oscillating neural system.

4 | CONCLUSION

We fully agree with Doelling and Assaneo (2021) that oscillations are a “start rather than the end to understanding brain activity.” Nevertheless, we have to reach that start. Finding an answer to “oscillation or not” is therefore important and satisfying per se and will guide the biophysical modelling and theory building that the authors propose. Characterizing the dynamics underlying brain activity should go hand in hand with, rather than replace, testing for the presence of oscillators. Oscillation or not, we can know and need to know.

ACKNOWLEDGEMENTS

A.A. is supported via the Agence Nationale de la Recherche, and B.Z. is supported via the Centre National de la Recherche Scientifique.

CONFLICT OF INTEREST

The authors declare no competing interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ejn.15542>.

ORCID

Sander van Bree  <https://orcid.org/0000-0003-4894-5938>

Andrea Alamia  <https://orcid.org/0000-0001-9826-2161>

Benedikt Zoefel  <https://orcid.org/0000-0002-9800-2551>

REFERENCES

- Biau, E., Wang, D., Park, H., Jensen, O., & Hanslmayr, S. (2021). Auditory detection is modulated by theta phase of silent lip movements. *Current Research in Neurobiology*, 2, 100014. <https://doi.org/10.1016/j.crneur.2021.100014>
- Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science (New York, N.Y.)*, 304(5679), 1926–1929. <https://doi.org/10.1126/science.1099745>
- Doelling, K. B., & Assaneo, M. F. (2021). Neural oscillations are a start toward understanding brain activity rather than the end. *PLoS Biology*, 19(5), e3001234. <https://doi.org/10.1371/journal.pbio.3001234>
- Fries, P. (2015). Rhythms for cognition: Communication through coherence. *Neuron*, 88(1), 220–235. <https://doi.org/10.1016/j.neuron.2015.09.034>
- Fröhlich, F. (2015). Experiments and models of cortical oscillations as a target for noninvasive brain stimulation. *Progress in Brain Research*, 222, 41–73. <https://doi.org/10.1016/bs.pbr.2015.07.025>
- Huang, W. A., Stitt, I. M., Negahbani, E., Passey, D. J., Ahn, S., Davey, M., Dannhauer, M., Doan, T. T., Hoover, A. C., Peterchev, A. V., Radtke-Schuller, S., & Fröhlich, F. (2021). Transcranial alternating current stimulation entrains alpha oscillations by preferential phase synchronization of fast-spiking cortical neurons to stimulation waveform. *Nature Communications*, 12(1), 3151. <https://doi.org/10.1038/s41467-021-23021-2>
- Hutcheon, B., & Yarom, Y. (2000). Resonance, oscillation and the intrinsic frequency preferences of neurons. *Trends in Neurosciences*, 23(5), 216–222. [https://doi.org/10.1016/s0166-2236\(00\)01547-2](https://doi.org/10.1016/s0166-2236(00)01547-2)
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science (New York, N.Y.)*, 320(5872), 110–113. <https://doi.org/10.1126/science.1154735>
- Llinás, R. R. (1988). The intrinsic electrophysiological properties of mammalian neurons: Insights into central nervous system function. *Science (New York, N.Y.)*, 242(4886), 1654–1664. <https://doi.org/10.1126/science.3059497>
- Lozano-Soldevilla, D., ter Huurne, N., Cools, R., & Jensen, O. (2014). GABAergic modulation of visual gamma and alpha oscillations and its consequences for working memory performance. *Current Biology*, 24(24), 2878–2887. <https://doi.org/10.1016/j.cub.2014.10.017>
- Pikovsky, A., Kurths, J., Rosenblum, M., & Kurths, J. (2003). *Synchronization: A universal concept in nonlinear sciences*. Cambridge University Press. <https://doi.org/10.1007/978-94-010-0217-2>
- Singer, W. (2018). Neuronal oscillations: Unavoidable and useful? *European Journal of Neuroscience*, 48(7), 2389–2398. <https://doi.org/10.1111/ejn.13796>
- van Bree, S., Sohoglu, E., Davis, M. H., & Zoefel, B. (2021). Sustained neural rhythms reveal endogenous oscillations supporting speech perception. *PLoS Biology*, 19(2), e3001142. <https://doi.org/10.1371/journal.pbio.3001142>
- Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*, 7(12), 553–559. <https://doi.org/10.1016/j.tics.2003.10.012>

- Womelsdorf, T., Valiante, T. A., Sahin, N. T., Miller, K. J., & Tiesinga, P. (2014). Dynamic circuit motifs underlying rhythmic gain control, gating and integration. *Nature Neuroscience*, *17*(8), 1031–1039. <https://doi.org/10.1038/nn.3764>
- Zoefel, B., ten Oever, S., & Sack, A. T. (2018). The involvement of endogenous neural oscillations in the processing of rhythmic input: More than a regular repetition of evoked neural responses. *Frontiers in Neuroscience*, *12*, 95. <https://doi.org/10.3389/fnins.2018.00095>

How to cite this article: van Bree, S., Alamia, A., & Zoefel, B. (2022). Oscillation or not—Why we can and need to know (commentary on Doelling and Assaneo, 2021). *European Journal of Neuroscience*, *55*(1), 201–204. <https://doi.org/10.1111/ejn.15542>