HHS Public Access
Author manuscript
*Lang Cogn Neurosci*. Author manuscript; available in PMC 2021 March 12.

Published in final edited form as:
*Lang Cogn Neurosci*. 2020 ; 35(9): 1119–1123. doi:10.1080/23273798.2020.1758335.

# Entrainment revisited: a commentary on Meyer, Sun & Martin (2020)

**Saskia Haegens**[1,2]

[1.] Department of Psychiatry, Division of Systems Neuroscience, Columbia University and the Research Foundation for Mental Hygiene, New York State Psychiatric Institute, New York, NY, USA [2.] Donders Institute for Brain, Cognition and Behaviour, Centre for Cognitive Neuroimaging, Radboud University Nijmegen, Nijmegen, The Netherlands

## Brain oscillations

Almost a century ago, Bishop proposed that brain oscillations reflect rhythmic fluctuations of neuronal populations between high and low excitability states (Bishop, 1932). While the implications of this fundamental proposition are still actively debated, a large body of research supports the idea that oscillations are instrumental rather than incidental to brain operations (for review, see, e.g., Buzsáki, 2006; Schroeder and Lakatos, 2009; Wang, 2010).

Several studies have shown that the phase of intrinsic low-frequency oscillations (<10 Hz) in the sensory cortices predicts both the size of the neural response and perceptual performance following sensory input, especially in the case of near-threshold stimulus detection (Ai and Ro, 2014; Busch, Dubois, & VanRullen, 2009; Henry, Herrmann, & Obleser, 2016; Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). This dynamic is further captured by the idea that (spontaneous) oscillations rhythmically sample sensory inputs (VanRullen, 2016; VanRullen, Busch, Drewes, & Dubois, 2011) and cause rhythmic fluctuations in performance (Fiebelkorn et al., 2011; Fiebelkorn, Saalmann, & Kastner, 2013; Landau and Fries, 2012; Landau, Schreyer, van Pelt, & Fries, 2015).

Furthermore, when the brain is presented with a rhythmic input stream, it tends to produce a rhythmic response. Indeed, there is a striking match between the rhythmic structures of many natural, behaviourally-relevant events (speech being a prime example) and those of intrinsic brain oscillations (Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008; Zion Golumbic et al., 2013). This observation has inspired the proposal that intrinsic brain oscillations might synchronize—or entrain—with external rhythms, and that such entrainment might facilitate sensory processing (and perhaps even higher-level processing) of further inputs that occur in-sync (i.e., on beat) with this rhythm (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). The key idea is that if the high-excitability phase of oscillations can be adjusted to coincide with task-relevant sensory input—either in an automatic, bottom-up fashion or through mechanisms of temporal prediction (Nobre, Correa, & Coull, 2007)—this input would undergo optimal processing (Haegens and Zion Golumbic, 2018; Large and Jones, 1999; Schroeder and Lakatos, 2009). This intuitively appealing idea has inspired many recent studies examining the involvement of neural oscillations in perceptual processing, and has received substantial theoretical support (Herbst and Landau, 2016; Schroeder and Lakatos, 2009; Schroeder, et al., 2008; Thut, Schyns, & Gross, 2011; VanRullen, 2016). One field of study that has embraced this idea is that of speech processing and language comprehension.

## Entrainment?

In their review article "*Synchronous, but not entrained: exogenous and endogenous cortical rhythms of speech and language processing*", Meyer, Sun & Martin (2020) criticize the almost singular focus entrainment has received recently, and argue that in fact entrainment might not provide a full account of speech processing. This critical re-assessment of entrainment fits into a larger picture of recent opinion pieces evaluating the entrainment framework (Haegens and Zion Golumbic, 2018; Helfrich, Breska, & Knight, 2019; Lakatos, Gross, & Thut, 2019; Obleser and Kayser, 2019; Rimmele, Morillon, Poeppel, & Arnal, 2018; Zoefel, ten Oever, & Sack, 2018).

Meyer et al. address two main challenges of the entrainment account: (1) that speech is in fact not strictly rhythmic—an often overlooked issue that is especially problematic when assigning (temporally) "predictive" properties to entrainment; and (2) that synchronization can happen in the absence of a rhythm being physically present in the input stimulus. An example of the latter would be "entrainment" to word rate: since in natural speech there are no physical word boundaries (i.e., a power spectrum of the acoustic input would not contain a peak at the word rate), it is not clear what external rhythm the brain would be "entraining" to. Meyer et al. argue that at least part of the observations currently being attributed to entrainment, might actually reflect intrinsic synchronization rather than alignment with an external rhythm. They suggest that while some of the observed phenomena might indeed reflect entrainment to exogenous, rhythmic acoustic information, a substantial part of it might instead be due to endogenous rhythmic processes reflecting, e.g., linguistic inference.

Meyer et al. use the term "entrainment proper" to denote synchronizing of brain rhythms in the sensory systems with rhythmic stimulus features. This resonates with a recent proposal by Haegens and Zion Golumbic (2018), where we argued for perhaps an even stricter definition requiring further empirical evidence: (1) presence of endogenous oscillatory activity in the absence of rhythmic stimulation; (2) phase-alignment of these intrinsic oscillators with external rhythmic input—here a crucial additional requirement is frequency selectivity, i.e., this coupling behaviour should only occur for a range of rhythms near the oscillator's intrinsic rate or eigenfrequency, not for all possible input frequencies (since that type of following could be accomplished by a passive linear system); and (3) a continuation of this oscillatory activity for at least a number of cycles beyond the external input (i.e., reverberation; tentatively shown by, e.g., Kösem et al., 2018; Lakatos et al., 2013), after which dampening or return to the original state may occur. Note that the second requirement might be very difficult to prove, since it is not trivial to separate a series of evoked responses (which after spectral analysis will produce a peak at the frequency of the input rhythm) from "genuine" oscillatory activity (for potential analytical approach to this, with in fact conflicting conclusions, see Capilla, Pazo-Alvarez, Darriba, Campo, & Gross, 2011; Notbohm, Kurths, & Herrmann, 2016).

Recently, Obleser and Kayser (2019) similarly proposed to distinguish between entrainment in the narrow vs. broad sense, with the former referring to genuine synchronization of internal and external rhythms, and the latter to any type of rhythmic response, including, e.g., a series of evoked impulse responses where no true oscillatory processes are involved. Helfrich, et al. (2019) similarly distinguish several processes that could be mistaken for entrainment, including superposition of evoked responses, top-down endogenous predictions, and resonance. The latter refers to a perturbation of a system after which it starts oscillating at its eigenfrequency (followed by dampening); such a perturbation could be a singular event or a rhythmic input, and the system could be at rest (i.e., not in an oscillatory state) prior to it. Based on brain activity measured during rhythmic stimulation, it would be very difficult to analytically distinguish between entrainment and any of these alternative explanations. Furthermore, and in a similar way, synchronized activity measured right after a rhythmic input could be due to any of these phenomena. Another hard-to-distinguish alternative account is a general phase-reset of ongoing oscillatory activity with each input (including with each pulse in a rhythmic input stream). This would lead to increased synchronization of all intrinsic oscillators, not just the ones that happen to match the input rhythm (Wilsch, Mercier, Obleser, Schroeder, & Haegens, in press); however, considering overlap in intrinsic and naturally occurring extrinsic rhythms (plus perhaps some blurring in the spectral analysis), this could easily be mistaken for reverberation following "entrainment".

As should be apparent from this discussion, the Meyer et al. review is very much in line with several recent critical pieces on the entrainment account (Breska and Deouell, 2017; Haegens and Zion Golumbic, 2018; Helfrich, et al., 2019; Obleser and Kayser, 2019). While indeed intuitively appealing, the claim that entrainment is the mechanism underlying speech and language processing still lacks a thorough empirical foundation; a foundation which, as a field, I believe we need to deliver in order to move our understanding of the potential mechanistic role of oscillations further. More fundamentally, as a field, we should be much clearer and more precise in what exactly we mean when we talk about entrainment. I contend that the term entrainment, as borrowed from dynamical systems theory (Pikovsky, Rosenblum, & Kurths, 2003), should be used in a strict sense (Haegens and Zion Golumbic, 2018; Helfrich, et al., 2019; Obleser and Kayser, 2019). If the required evidence that goes with this narrow definition (as listed above) is not there, we should perhaps use a different term for the rhythmic phenomena we are observing, rather than invoking a set of implied assumptions for which there is no basis. Perhaps the rhythmic response to rhythmic input should be referred to as *rhythmic tracking*. This, I argue, is a more neutral term that might encompass oscillatory as well as non-oscillatory mechanisms; it captures any close following of rhythmic input resulting in a rhythmic pattern in brain activity, but does not necessarily involve phase-alignment of genuine oscillations that intrinsically existed before and will continue to exist for X amount of time beyond the external rhythm. Rhythmic tracking—note that Obleser and Kayser (2019) refer to this same concept as *neural tracking* or *entrainment in the broad sense*—comes with less implications than (often implicitly) invited by using the term entrainment: as it does not imply continuation beyond the rhythmic input, no ambiguous suggestions of prediction, inference, or other top-down processes are made.

## Future dynamics

With their focus on endogenous rhythmicity and the role this intrinsic synchronization might play in various higher-level processes, Meyer et al. provide the field of speech and language processing with a clear suggestion for future research. A critical next step would be to develop empirical paradigms and analytical tools that can deliver on that front. Generally speaking for the oscillations field, I believe our research focus should be on mechanistic understanding, including the generation, underlying physiology, and, critically, the potential causal role of these oscillatory dynamics. That is where the real challenges and opportunities reside, and where, in this author's opinion, we are currently falling short. To quote Obleser and Kayser (2019): "Unfortunately, the analytical advances of recent years have not yet brought us much closer to a cause-and-effect-like ('mechanistic') understanding of how entrainment (in the narrow or broad sense) represents a necessary and/or sufficient neurobiological substrate for the human faculty of language." There is no doubt that the brain produces rhythmic activity, and that these rhythmic dynamics at the very least correlate with various behavioural states. However, a large gap exists in our understanding linking these elements. In other words, we need to connect the how and what (Martin, 2016).

Over the last two decades, we have seen a shift in neuroscience from the traditional focus on the brain's (passive) response to stimuli, to the study of (anticipatory) activity prior to sensory input. This shift in paradigm from the brain as a stimulus-response device to the brain as a dynamical system has led to an exciting transition in our understanding of neuronal processing. Ideas such as *predictive coding* (Rao and Ballard, 1999) and *active sensing* (Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010) reflect this shift, with a proposed leading role for brain oscillations (e.g., Bastos et al., 2012; Buzsáki, 2019; Martin, 2020). Thoroughly testing these ideas and the proposed causal roles for oscillatory dynamics will be important next steps.

To give one example: as Meyer et al. discuss, beta band oscillations have been linked to both auditory and linguistic predictability (e.g., Merchant, Grahn, Trainor, Rohrmeier, & Fitch, 2015), and have been proposed to subserve the generation of predictions both in linguistic context and more generally in the predictive coding literature (e.g., Chao, Takaura, Wang, Fujii, & Dehaene, 2018). This directly connects to a recent proposal that beta oscillations reflect transient, flexible ensemble formation, observed specifically in the context of endogenous content (re-)activation (Spitzer and Haegens, 2017). Such a framework provides a potential avenue for future research, focusing on a particular mechanistic role for oscillatory activity, at least in theory allowing the linking of say information encoding in spike firing patterns to behavioural outcomes.

To conclude, a large body of research suggests that oscillations play a fundamental role in perception and cognition, including speech and language processing. As Meyer et al. critically point out, this rhythmicity might to a large extent be endogenously driven, and key to our understanding of brain function. The brain does not passively follow external input, and also does not consist of singular simple oscillators. Rather, it is a complex dynamical system, with one of its emergent properties being oscillatory activity. Understanding these complex dynamics will bring us closer to an understanding of cognitive function, including language comprehension. Moving beyond simplistic dogma will be key for the future of our field.

## Acknowledgements

The author thanks Laura Gwilliams and Luca Iemi for helpful feedback on an earlier version. This work was supported by NWO Vidi grant 016.Vidi.185.137 and by NIH grant P50-MH109429.

## REFERENCES

Ai L, & Ro T (2014). The phase of prestimulus alpha oscillations affects tactile perception. Journal of Neurophysiology, 111(6), pp. 1300–1307. [PubMed: 24381028]

Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, & Friston KJ (2012). Canonical microcircuits for predictive coding. Neuron, 76(4), pp. 695–711. [PubMed: 23177956]

Bishop GH (1932). Cyclic changes in excitability of the optic pathway of the rabbit. American Journal of Physiology, 103(1), pp. 213–224.

Breska A, & Deouell LY (2017). Neural mechanisms of rhythm-based temporal prediction: Delta phase-locking reflects temporal predictability but not rhythmic entrainment. PLoS Biology, pp. 1–24.

Busch NA, Dubois J, & VanRullen R (2009). The phase of ongoing EEG oscillations predicts visual perception. Journal of Neuroscience, 29(24), pp. 7869–7876. [PubMed: 19535598]

Buzsáki G (2006). Rhythms of the brain: Oxford University Press.

Buzsáki G (2019). The brain from inside out: Oxford University Press.

Capilla A, Pazo-Alvarez P, Darriba A, Campo P, & Gross J (2011). Steady-state visual evoked potentials can be explained by temporal superposition of transient event-related responses. PLoS ONE, 6(1), pp. e14543–14515. [PubMed: 21267081]

Chao ZC, Takaura K, Wang L, Fujii N, & Dehaene S (2018). Large-scale cortical networks for hierarchical prediction and prediction error in the primate brain. Neuron, 100(5), pp. 1252–1266.e1253. [PubMed: 30482692]

Fiebelkorn IC, Foxe JJ, Butler JS, Mercier MR, Snyder AC, & Molholm S (2011). Ready, set, reset: Stimulus-locked periodicity in behavioral performance demonstrates the consequences of cross-sensory phase reset. Journal of Neuroscience, 31(27), pp. 9971–9981. [PubMed: 21734288]

Fiebelkorn IC, Saalmann YB, & Kastner S (2013). Rhythmic sampling within and between objects despite sustained attention at a cued location. Current Biology, 23(24), pp. 2553–2558. [PubMed: 24316204]

Haegens S, & Zion Golumbic E (2018). Rhythmic facilitation of sensory processing: A critical review. *Neuroscience &* Biobehavioral Reviews, 86, pp. 150–165.

Helfrich RF, Breska A, & Knight RT (2019). Neural entrainment and network resonance in support of top-down guided attention. Current Opinion in Psychology, 29, pp. 82–89. [PubMed: 30690228]

Henry MJ, Herrmann B, & Obleser J (2016). Neural microstates govern perception of auditory input without rhythmic structure. Journal of Neuroscience, 36(3), pp. 860–871. [PubMed: 26791216]

Herbst SK, & Landau AN (2016). Rhythms for cognition: the case of temporal processing. Current Opinion in Behavioral Sciences, 8, pp. 85–93.

Kösem A, Bosker HR, Takashima A, Meyer A, Jensen O, & Hagoort P (2018). Neural entrainment determines the words we hear. Current Biology, 28(18), pp. 2867–2875.e2863. [PubMed: 30197083]

Lakatos P, Chen CM, O'Connell MN, Mills A, & Schroeder CE (2007). Neuronal oscillations and multisensory interaction in primary auditory cortex. Neuron, 53(2), pp. 279–292. [PubMed: 17224408]

Lakatos P, Gross J, & Thut G (2019). A new unifying account of the roles of neuronal entrainment. Current Biology, 29(18), pp. R890–R905. [PubMed: 31550478]

Lakatos P, Karmos G, Mehta AD, Ulbert I, & Schroeder CE (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. Science, 320(5872), pp. 110–113. [PubMed: 18388295]

Lakatos P, Musacchia G, O Connel, Monica N, Falchier, Arnaud Y, Javitt, Daniel C, & Schroeder, Charles E. (2013). The spectrotemporal filter mechanism of auditory selective attention. Neuron, 77(4), pp. 750–761. [PubMed: 23439126]

Landau AN, & Fries P (2012). Attention samples stimuli rhythmically. Current Biology, pp. 1–5.

Landau AN, Schreyer HM, van Pelt S, & Fries P (2015). Distributed attention is implemented through theta- rhythmic gamma modulation. Current Biology, pp. 1–19.

Large EW, & Jones MR (1999). The dynamics of attending: How people track time-varying events. Psychological Review, 106(1)

Martin AE (2016). Language processing as cue integration: Grounding the psychology of language in perception and neurophysiology. Frontiers in Psychology, 7(120)

Martin AE (2020). A compositional neural architecture for language. Journal of Cognitive Neuroscience

Mathewson KE, Gratton G, Fabiani M, Beck DM, & Ro T (2009). To see or not to see: Prestimulus alpha phase predicts visual awareness. Journal of Neuroscience, 29(9), pp. 2725–2732. [PubMed: 19261866]

Merchant H, Grahn J, Trainor L, Rohrmeier M, & Fitch WT (2015). Finding the beat: a neural perspective across humans and non-human primates. Philosophical Transactions of the Royal Society B: Biological Sciences, 370(1664)

Meyer L, Sun Y, & Martin AE (2020). Synchronous, but not entrained: exogenous and endogenous cortical rhythms of speech and language processing. Language, Cognition and Neuroscience, pp. 1–11. [PubMed: 32449872]

Nobre AC, Correa A, & Coull JT (2007). The hazards of time. Current Opinion in Neurobiology, 17(4), pp. 465–470. [PubMed: 17709239]

Notbohm A, Kurths J, & Herrmann CS (2016). Modification of brain oscillations via rhythmic light stimulation provides evidence for entrainment but not for superposition of event-related responses. Frontiers in Human Neuroscience, 10(10)

Obleser J, & Kayser C (2019). Neural entrainment and attentional selection in the listening brain. Trends in Cognitive Sciences, pp. 1–14.

Pikovsky A, Rosenblum M, & Kurths J (2003). Synchronization: A universal concept in nonlinear sciences (First ed.): Cambridge University Press.

Rao RP, & Ballard DH (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nature Neuroscience, 2(1), pp. 79–87. [PubMed: 10195184]

Rimmele JM, Morillon B, Poeppel D, & Arnal LH (2018). Proactive sensing of periodic and aperiodic auditory patterns. Trends in Cognitive Sciences, 22(10), pp. 870–882. [PubMed: 30266147]

Schroeder CE, & Lakatos P (2009). Low-frequency neuronal oscillations as instruments of sensory selection. Trends in Neurosciences, 32(1), pp. 9–18. [PubMed: 19012975]

Schroeder CE, Lakatos P, Kajikawa Y, Partan S, & Puce A (2008). Neuronal oscillations and visual amplification of speech. Trends in Cognitive Sciences, 12(3), pp. 106–113. [PubMed: 18280772]

Schroeder CE, Wilson DA, Radman T, Scharfman H, & Lakatos P (2010). Dynamics of active sensing and perceptual selection. Current Opinion in Neurobiology, 20(2), pp. 172–176. [PubMed: 20307966]

Spitzer B, & Haegens S (2017). Beyond the status quo: A role for beta oscillations in endogenous content (re)activation. eNeuro, 4(4)

Thut G, Schyns PG, & Gross J (2011). Entrainment of perceptually relevant brain oscillations by non-invasive rhythmic stimulation of the human brain. Frontiers in Psychology, 2(170)

VanRullen R (2016). Perceptual cycles. Trends in Cognitive Sciences, pp. 1–13.

VanRullen R, Busch N, Drewes J, & Dubois J (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Frontiers in Psychology, 2(60)

Wang X-J (2010). Neurophysiological and computational principles of cortical rhythms in cognition. Physiological Reviews, 90(3), pp. 1195–1268. [PubMed: 20664082]

Wilsch A, Mercier M, Obleser J, Schroeder CE, & Haegens S (in press). Spatial attention and temporal expectation exert differential effects on visual and auditory discrimination. Journal of Cognitive Neuroscience

Zion Golumbic EM, Ding N, Bickel S, Lakatos P, Schevon CA, McKhann GM, … Schroeder CE. (2013). Mechanisms underlying selective neuronal tracking of attended speech at a “cocktail party”. Neuron, 77(5), pp. 980–991. [PubMed: 23473326]

Zoefel B, ten Oever S, & Sack AT (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)