Decoupling Measurements and Processes: On the Epiphenomenon Debate Surrounding Brain Oscillations in Field Potentials

Authors

Sander van Bree[1,2,3]*, Daniel Levenstein[4,5], Matthew R. Krause[5], Bradley Voytek[6], Richard Gao[7]*†

1 Department of Medicine, Justus Liebig University, Giessen, Germany
2 Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
3 Centre for Cognitive Neuroimaging, School of Psychology and Neuroscience, University of Glasgow, Glasgow, United Kingdom
4 MILA – Quebec AI Institute, Montreal, Canada
5 Montreal Neurological Institute and Hospital, McGill University, Montreal, Canada
6 Department of Cognitive Science, Halıcıoğlu Data Science Institute, University of California, San Diego, La Jolla, USA
7 Machine Learning in Science, Excellence Cluster Machine Learning and Tübingen AI Center, University of Tübingen, Tübingen, Germany

* These authors contributed equally to this work
† Corresponding author: r.dg.gao@gmail.com

Abstract

Various theories in neuroscience maintain that brain oscillations have an important role in neuronal computation, but opposing views claim that these macroscale dynamics are “exhaust fumes” of more relevant processes. Here, we argue that the question of whether oscillations are epiphenomenal is ill-defined and cannot be productively resolved without further refinement. Toward that end, we outline a conceptual framework that clarifies the dispute along two axes: first, we introduce a distinction between measurement and process to categorize the theoretical status of electrophysiology terms such as local field potentials and oscillations. Second, we consider the relationships between these disambiguated terms, evaluating based on experimental and computational evidence whether there exist causal or inferentially useful links between them. This decomposes the question of epiphenomenalism into a set of empirically tractable alternatives. Finally, we demarcate oscillations as a conceptually distinct entity where either processes or measurements exhibit periodic behavior, and we suggest that oscillatory processes orchestrate neural computation by implementing a temporal, spatial, and frequency syntax. Overall, our reframed evaluation supports the view that electric fields—oscillating or not—are causally relevant, and that their associated signals are informative. More broadly, we offer a vocabulary and starting point for scientific exchanges on the role and utility of brain signals and the biological processes they capture.

Keywords: electrophysiology, neural oscillations, local field potential, measurement, process, causality, conceptual analysis

1. Introduction

Since nearly a century ago, neuroscientists have observed that aggregate neural signals, measured as electroencephalography (EEG), magnetoencephalography (MEG), and local field potential (LFP) recordings show regular fluctuations at characteristic frequencies (Berger, 1929; Loomis et al., 1938). The presence and characteristics of these *oscillations* correlate with various aspects of cognition and behavior (Vanderwolf, 1969; Clayton et al., 2015; Ward, 2003; Herweg et al., 2020; Khanna & Carmena, 2015), raising the possibility that they play a causal role in neural information processing. This hypothesis has given rise to a highly productive research program in which oscillations are cast as coordinators or orchestrators of brain activity (Buzsáki, 2010; Fries, 2005).

However, a competing view is that oscillations, and electric field potentials more broadly, are merely byproducts of neural computation. Under this alternative, oscillations passively reflect neuronal spiking without influencing neuronal computation itself. The contrast between these two perspectives manifests most sharply in the question of whether oscillations in LFPs are epiphenomenal, and its resolution has potentially important implications on the explanatory primacy of spikes versus aggregate macroscale brain activity in theories of cognition (Barack & Krakauer, 2021), as well as the merit of frameworks that grant brain oscillations an active role (Buzsáki & Draguhn, 2004).

In this manuscript, we argue that the question of whether oscillations and LFPs are epiphenomenal is ill-defined. Specifically, each concept in this question (oscillations, LFPs, and epiphenomenal) has multiple meanings. As a result, they must be disentangled in order for testable hypotheses to emerge. Here, we outline a conceptual framework that disambiguates the question by reformulating it into a set of more precise alternatives, which we hope would make disputes on the importance of neural signals more empirically tractable. Furthermore, we offer preliminary answers to the reformulated questions using experimental and computational evidence.

This contribution unfolds as follows. First, we introduce a distinction between **processes** and **measurements**, which we use to classify key concepts in the electrophysiology literature (Section 2). Second, we introduce two criteria that can be used to evaluate the *relationship* between such concepts (Section 3):

(1) The **inference** criterion: Which entity is *informative* toward which other entity?

(2) The **causality** criterion: Which entity is *causal* toward which other entity?

Leveraging this framework, we then consider the links between LFPs, neurobiological processes, cognition and behavior (Section 4), with oscillations considered separately in light of their unique causal and inferential role (Section 5). We end by offering concluding remarks, and by defending the general applicability of our framework (Section 6).

2. Measurements and Processes

One key distinction that must be made in scientific practice is between measurements and processes. Where **process** refers to physical objects and events in the world which are the targets of our investigations, **measurements** refer to the signals or recordings we use to capture information about such objects and events (see Table 1 for a glossary).

Examples of **processes** in neuroscience are *neurobiological events* across spatiotemporal scales, including action potentials, molecular cascades, inter-ensemble communication, and any other dynamic interaction between neural structures occurring from the molecular scale to the scale of anatomical regions (Bassett & Sporns, 2017) and distributed networks (Pessoa, 2023). Furthermore, forms of behavior such as motor activity are also physical processes with possible causal effects, as are cognitive processes like attention.

Measurements qualitatively or quantitatively capture processes with the goal of generating scientific inferences about them. Here, we use measurement in noun form (i.e., roughly synonymous with terms like signal or recording) rather than as a verb, which refers to the act of measurement (see Tiruvadi, 2023 for a relevant discussion). While one might argue that measurements are themselves processes, they are privileged from the perspective of scientific investigation in that they are processes designed and used for inference about other processes, rather than being objects of study themselves.

The primary term of interest pertaining to the ill-defined question raised in the introduction is the electric field potential, which we categorize as a measurement. Specifically, the field potential refers to a signal that quantifies the voltage difference between an electrode at a location of interest and a spatially separate reference electrode (Anastassiou et al., 2011). Such potentials can be *local* or *global*. *Local* field potentials are recordings in extracellular space using electrodes inside the brain. *Global* field potentials are recordings using non-invasive techniques such as EEG, or magnetically using MEG, which capture the interaction of many sources throughout the brain simultaneously. We might also add a *mesoscale* for intermediate levels, such as recordings on the cortical surface (electrocorticography; ECoG).

For local field potential recordings, a standard practice is to separate the raw signal into two components via analog or digital filters. The first component comprises frequencies below 1000 Hertz (Hz), which usually retains the same name of LFP (which might cause terminological ambiguity in its own right). The second component comprises frequencies between roughly 300 and 3000 Hz, which are separately processed for applications such as spike detection and inferences about single-neuron action potentials.

Thus, spikes and LFPs are signals that originate from the same voltage recordings, filtered in such a way to hone in on the respective process that stereotypically (but not necessarily) underpins each. Specifically, spikes tap into *action potentials*, and local and global field potentials reflect *aggregate electric fields*, which are charged particles moving through space (such as across neuronal membranes). Both action potentials and electric fields (henceforth *e-fields*) are processes that can in principle exert causal effects on subsequent neural events, but measurements thereof cannot. One intuitive way to parse the distinction between measurement and process is to consider the role of reference electrodes: the location and physical properties of reference electrodes, as well as the applied referencing scheme changes measurements (Buzsáki et al., 2012; Einevoll et al., 2013; Shirhatti et al., 2016), but e-fields, action potentials, and other physical processes are there and the same regardless of whether there are electrodes to measure them in the first place. For the remainder of our analysis, we focus on LFPs, with most of the conclusions carrying over to global field potentials unless stated otherwise.

Table 1: Glossary of key terms

Term	Definition
Measurement	A recording or signal that captures information about a physical process, offering a qualitative or quantitative indication of changes to this process; e.g., a time series of voltage values
Process	Physical events in the world which may be observed through a measurement; e.g., the movement of ions and proteins, but we also include static entities such as an axon
Field potential (local/global)	Voltage recordings of electric fields measured locally in extracellular space (LFP) or globally from masses of activity (EEG, or detection of their magnetic fields using MEG). All field potentials are *measurements*
Electric field	Physical field of charged particles, whose movement (a *process*) is captured by field potential recordings (*a measurement*)
Spike	*As a measurement*: Sharp deflections in the high-pass filtered LFP, lasting ~1ms in duration and often with a stereotypical waveform across neighboring recording channels *As a process*: An action potential, or the rapid change in electrical potential associated with the passage of an impulse along the membrane of a neuron, caused by the opening and closing of sodium and potassium channels
Oscillation	*As a measurement*: Periodic structure in the LFP, commonly detected by bandpass filtering or observing peaks in the power spectrum *As a process*: Periodic structure in the brain's electric fields, neurobiological processes (e.g., synaptic events), behavior, or any other process resulting from an oscillator mechanism (for details, see Section 5.2)
Ephaptic coupling	A process in which extracellular e-fields influence neurons, and in particular, their membrane voltage potential, via non-synaptic and non-gap junction means
Epiphenomenon	Events that are caused by processes in a system but which do not exert causal effects on the system itself, such as the steam whistle of a locomotive relative to its movement
Causal relation	A relation between A and B is causal if there is a possible intervention on A that produces changes in B or vice versa, such as when an experimental lesion of a brain region impairs a cognitive function

3. Disentangling inference and causality

We next add two additional criteria: to what extent are LFPs, oscillations, and electric fields *causally relevant*, and to what extent are they *inferentially informative*?

The **inference** criterion is epistemic. Here, the question is whether information about one entity reduces uncertainty about the state of another. For example, if we see oscillations in the LFP at a specific frequency band, does this lower our uncertainty about which cognitive processes are currently active, or which neurobiological processes are ongoing? Even if no direct causal link underpins any two processes, a measurement of one may still confer information about the other.

The **causality** criterion considers whether any one entity influences another. For the present purposes, we define a causal relationship as one where interventions on one entity can in principle produce changes in another (Woodward, 2003; Pearl, 2009; see Barack et al., 2022 & Ross & Bassett, 2024 for relevant discussions).

Together with measurements and processes, the distinction between inference and causality offers a disambiguation tool which we can use to sharpen our analysis, setting the stage for further inquiry. In the writing that follows, we first evaluate the causal and inference criteria of the *LFP* and the *e-field* in relation to *neurobiological processes* and *behavior*, regardless of the specific temporal dynamics at play (Section 4). After that, we turn to *oscillations* specifically, which we argue can occur both in measurement and process, and which are poised to serve a general computational role in the brain (Section 5).

4. Theoretical status of local field potential and electric fields

In this section, we introduce a roadmap to understanding the relationship between various key terms in the electrophysiology literature, evaluating their links via the criteria of causality and inference. For an overview of our conceptual framework, see Figure 1. Now, we unpack this roadmap and evaluate the questions it yields, starting with uncontentious ones and moving to increasingly complex relations.

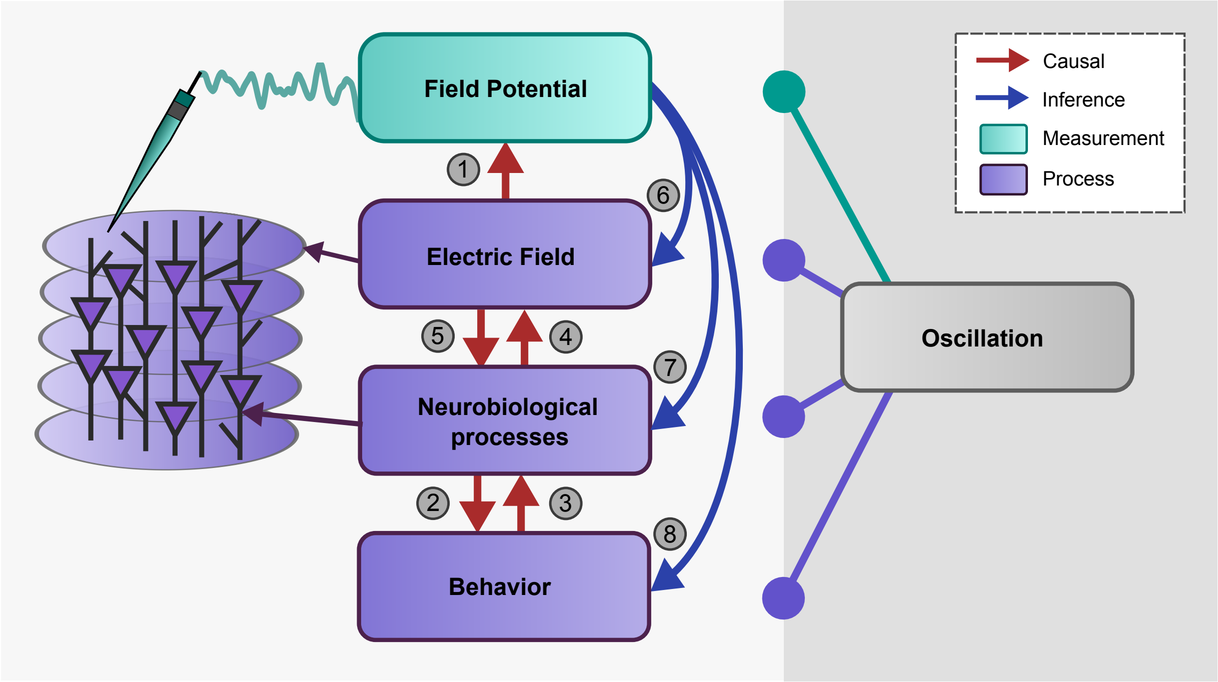

Figure 1. A conceptual roadmap for electrophysiology terms
In this framework, we separate four primary entities of interest. At the top, local and global field potentials measure e-fields without itself exerting any causal effects on the brain (cyan). One step down, the e-fields captured by this measurement are produced by neuronal activity and other electrochemical processes, and constitute a physical process (purple). Neurobiological processes in turn produce behavior and might be influenced by electric fields. Furthermore, each of the entities can display the

dynamical property of periodicity, instantiating a type of oscillation (right hand side)—a point which will be explicated in Section 5 and Figure 2. Arrows denote directions of causality (red) and informativeness (blue), and the numbers next to arrows are referred to in Section 4.

Are LFPs causal toward any entity?

No–the LFP is a measurement, which does not causally influence its underlying process.

*Are electric fields causal to the LFP? (**arrow 1**)*

Yes–as defined in Section 2, changes in extracellular e-fields sum up locally or globally to produce changes in microwires, EEG or ECoG electrodes, and which produce magnetic fields that are detected using MEG. This explains how the field potential signals come about. More technically, the negative gradient of the electric potential in any direction makes up the electric field component in that direction.

*Are neurobiological processes causal to behavior and vice versa? (**arrow 2 & 3**)*

Yes–axiomatic to the neurosciences, neurobiological processes influence behavior, either directly through efferent projections to the peripheral nervous system, or indirectly through long-lasting structural or functional changes which encode previous experience and future expectations. Conversely, behavior shapes sensory input available to the organism through for example active sensing (e.g., whisker movement) and bodily changes, thereby causally affecting neural processes.

*Are neurobiological processes causal to e-fields? (**arrow 4**)*

Yes–electric fields in the brain are both directly generated and indirectly shaped by neurobiological processes (Pesaran et al., 2018). Here, we provide some notable examples. First, as action potentials are initiated and propagated, a cascade of ion flow kicks in that changes electric gradients across neuronal segments. Second, neurotransmitter binding at postsynaptic sites opens membrane channels (e.g., chloride), with the associated charged ion movement altering the aggregate extracellular fields. Third, neuronal burst-firing is associated with slow calcium fluctuations (Teplov et al., 2021; Nestvogel & McCormick, 2022), which can change electric fields on a longer timescale (Krahe & Gabbiani, 2004). Out of these factors, it appears that the largest driver of extracellular electric fields are events near the synapse, as well as synchronous action potentials (Buzsáki et al., 2012; Einevoll et al., 2013; Mazzoni et al., 2015; Reimann et al., 2013). However, the exact distribution of causes is not fully mapped out, with further pursuits required (Buzsáki et al., 2012).

Besides the *generation* of e-fields, many neural events indirectly *influence* e-fields. For example, the morphology of nearby neurons, glial cells, and the electrical conductance of surrounding tissue affect the spatiotemporal structure of nearby e-fields (Bédard et al., 2006; Lindén et al., 2010). Together, these amount to biological filters that shape the e-field and the LFP measurements of it.

*Do e-fields causally influence neurobiological processes? (**arrow 5**)*

Our answer is a preliminary and tentative yes, though further work is needed to understand the nature and extent of these effects. Specifically, the available evidence points towards **ephaptic coupling**, a process by which extracellular e-fields, emanating from individual neurons, cell ensembles, or larger populations, exert causal influences on other neurobiological processes by routes other than direct synaptic transmission (Pinotsis et al., 2023). In our view, this is a pertinent reformulation of the question of whether LFPs are epiphenomenal because it turns the problem into an empirically tangible one about causal relations between operationalized processes.

Since neurons consist of polarizable cell membranes, it is a biophysical triviality that surrounding e-fields must polarize their membranes and thereby alter the neurons' excitability. Indeed, as a theoretical lower bound, neurons can be modulated by fields as weak as 0.01 V/m despite thermal and molecular shot noise (Weaver & Astumian, 1990; Weaver et al., 1999). However, the central question is whether there exist effects that are sufficiently strong to produce meaningful effects on neurobiological processes. Here we review experimental work suggesting that externally applied electrical fields produce changes in spiking activity at the field strengths produced by healthy brain activity. In parallel, computational work suggests that these principles also shape endogenous brain activity. We discuss both lines in turn.

First, the experimental induction of e-fields polarizes neurons both *in vitro* (Chan et al., 1988; Jefferys, 1995; Radman et al., 2007; Fröhlich & McCormick, 2010; Anastassiou et al., 2011) and *in vivo* (Vöröslakos et al., 2018). The direct effect of external fields on individual neurons is relatively small. Specifically, supplied fields generally polarize neuronal membranes by < 0.5 volt per meter (V/m) of the applied electrical field, although these effects may be somewhat amplified by resonance within a neural circuit (Ali et al., 2013). In addition to this, relatively strong e-fields (20 – 100 V/m) are required to evoke an action potential in quiescent neurons. A misconception is that because of these factors, weak fields such as less than 1 V/m are causally inefficacious. Importantly however, in evaluating whether exogenous e-fields produce neurobiological effects, action potential initiation is not the only bar. Namely, weak subthreshold input can alter the temporal structure of spike trains, inducing rhythmic regimes that cause neurons to fire sooner or later than they normally would (Anastassiou et al., 2011; Francis et al., 2003; Fröhlich & McCormick, 2010; Johnson et al., 2020; M. R. Krause et al., 2017, 2019; Ozen et al., 2010; Reato et al., 2010). As reviewed in Alekseichuk et al. (2022), external fields as weak as 0.5 V/m can alter the timing of neuronal spiking, with one study observing spike timing modulations at strengths as low as 0.2 V/m (Vieira et al., 2020).

The relevance of such findings depends on whether endogenous fields are similarly strong. As reviewed in Weiss & Faber (2010), a large body of work shows they are. Starting with a high bound, pathological discharges in the epileptic hippocampus can reach nearly 70 V/m (Jefferys, 1995). However, even healthy sharp-wave and ripple activity produce fields between 2 and 20 V/m (Ylinen et al., 1995). Furthermore, the structure of the hippocampus is well-suited to generate strong electric fields, and slow waves in the cortex produce e-fields of approximately 1 to 2 V/m (Weiss & Faber, 2010).

A limitation of the external field approach is that it perturbs the natural dynamics of neural systems. Computational models, in which properties and effects of neurally generated e-fields are simulated, offer a second line of support for ephaptic coupling. In one study, biophysical simulation of neuronal ensembles predicted LFP signals recorded during a spatial task better when the extracellular fields were modeled to weakly feed back into local neuron clusters (though not for all task conditions; Pinotsis & Miller, 2023). In another study, neural activity was found to propagate along an unfolded slice of hippocampus even when synaptic and gap junction transmission are blocked, with simulations tailored to the data suggesting that these effects emerge with biologically plausible field strengths (Zhang et al., 2014). Other efforts using in vitro and modeling-only approaches also support ephaptic coupling (Bokil et al., 2001; Qiu et al., 2015; Warman et al., 1992).

Furthermore, we highlight two promising future avenues. First, we can exploit propagation asymmetries between ephaptic and synaptic coupling mechanisms to get a handle on their relative causal contributions. While axons transmit signals at about 0.3 meters per second (m/s), synchronous e-fields propagate at around 0.1 m/s from their source (Qiu et al., 2015). As a result, during periodic regimes of neuronal activity, the two effects should interact and amplify at regular moments and distances, and their interference effects on neurobiological processes should be empirically discernible (Hesp, 2021). Second, we can apply pharmacological and genetic interventions that target bioelectric signaling pathways to acquire some direct control over endogenous fields and their dynamics (Levin, 2012, 2014).

In conclusion, these lines of evidence suggest endogenous electric fields are both sufficiently strong to alter neural activity (based on the effects of exogenous electric fields) and necessary to produce parsimonious accounts of some neural data. Thus, we believe that a common critique of ephaptic coupling—i.e., that it is simply too weak to produce meaningful effects—is unlikely to be true. Nevertheless, ephaptic effects may not be a major contributor to every brain circuit. Electric fields most effectively polarize a neuron when they are aligned with the cell's morphology, generally along its somatodendtric axis (Radman et al., 2009). One intriguing possibility is that some circuits may be organized in ways that minimize ephaptic input, akin to designs that mitigate crosstalk in engineered circuits. For example, cells near a large fiber bundle could be oriented orthogonally to the electric field it emits or have otherwise difficult-to-polarize morphology. Ephaptic and synaptic input also travel at different speeds (Qiu et al., 2015), and circuits could be specifically organized so that these signals either do or do not overlap. These are testable hypotheses which, to our knowledge, have not been systematically examined.

Do neural e-fields causally influence behavior? ***(no arrow)***

A further question is whether ephaptic coupling, if it is occurring endogenously in the brain, influences cognition. The causal stance on e-fields is that ephaptic effects are widespread and powerful enough to change information processing, cognition, and behavior. A non-causal stance on e-fields is that any association we find between the flow and charge of ions that make up neural e-fields and cognition results from other processes, in particular the processes that generated and influenced the e-field. As such, the non-causal view maintains that if any selective change were to occur to endogenous e-fields, no higher-level phenomena would be affected.

The answer to this dispute is actively being pursued, with indirect lines of evidence supporting the causal position. For one, weak external fields of 0.5 V/m increase measures of neuronal synchronization by similar amounts as observed during cognitive events such as working memory maintenance (Bahmani et al., 2018), learning on a discrimination task (Van Wingerden et al., 2010b), reward expectance (Van Wingerden et al., 2010a), and during other tasks (reviewed in M. R. Krause et al., 2019). Second, a growing body of research shows that externally induced electric fields influence human behavior across cognitive domains (Deng et al., 2019; Hanslmayr et al., 2019; V. Krause et al., 2016; Polanía et al., 2015; Thut et al., 2011; van Bree et al., 2021). To highlight an illustrative example, the application of an alternating current to frontal and parietal areas changes reaction times on a working memory task when the induced fields oscillate at specific frequencies (6 Hz but not 35 Hz), with such changes depending on the phase difference between the exogenous currents (Polanía et al., 2012). While causal results of this kind are encouraging, their implications toward the hypothesis that *endogenous* fields influence behavior and cognition relies on a complex and perhaps underexposed train of inference (Box 1; Bergmann & Hartwigsen, 2021).

Box 1: The interpretative logic of brain stimulation studies

As a general rule, brain stimulation studies adopt the following interpretive logic. First, a perturbational method is used to modulate an independent variable. For example, transcranial magnetic stimulation (TMS) or electric stimulation (tES) might be harnessed to control the presence or strength of a 10 Hz oscillatory field induced artificially in the parietal cortex. Then, it is measured how this manipulation alters a dependent variable, such as behavioral patterns in an attentional task. Finally, statistically reliable effects of the manipulation are taken to offer evidence that changes in endogenous analogues of the independent variable—for example, *internally* generated parietal alpha oscillations—also exert such causal effects on behavior. Critically, this inference contains a multitude of assumptions that warrant scrutiny. For example, to what extent are the supplied fields similar in voltage level and spatiotemporal dynamics to neurally generated e-fields (Ruffini et al., 2020)? What are the mechanisms by which the exogenous fields are hypothesized to exert their effect—standard interneural communication or ephaptic coupling—and is this how the naturally behaving brain realizes behavior too? What theoretical role do entities of interest play in accounting for the observed findings? For example, what causal and explanatory function is granted respectively to electric fields themselves, spikes, and population dynamics in accounting for the behavioral change? By moving such questions up front, we stand to gain more clarity on what brain stimulation results teach us about endogenous neural e-fields and their consequences for behavior, cognition, and neuronal computation.

Are LFPs informative of e-fields, neurobiological processes, and behavior?

Regardless of whether electric fields causally affect neurobiological processes or behavior, it is a further question whether their corresponding measurement, the LFP, offers information toward processes that can be used to gain scientific insights. Indeed, phrases like “causally relevant”, “epiphenomenon”, “exhaust fume”, and “byproduct” leave the extent to which field potential signals are scientifically meaningful open to interpretation. Here, we try to mitigate such underspecification by evaluating whether information about the state of any one framework entity reduces our uncertainty about the state of another.

*LFP to e-field (**arrow 6**)*

The LFP is deeply informative of e-fields because the charged ions that make up the e-field are what is directly picked up by electrodes. However, the measurement is imperfect and non-unique, given that it depends on the placement of the reference electrode. One technique to make LFP measurements invariant to such details is to compute the second spatial derivative of the signal. This recovers the current source density, affording near one-to-one inferences about the e-field (Bastos et al., 2018; Chen et al., 2011; Mitzdorf, 1985; Schroeder et al., 1995). Even then, LFP-to-field inferences are hampered by our ability to tell apart sink and source, as well as other noise factors such as electrode defects.

Two further interrelated issues are the inverse problem and source contamination. The inverse problem refers to the impossibility of finding a unique set of neuronal generators for any signal given insufficient observations, and the source contamination problem refers to the fact that e-fields other than the neural source of interest also influence the signal. These issues are most striking for global field potentials derived from EEG and MEG where many more neuronal sources explain variability in the signal, but they are a problem for local measurements too. With these limitations in mind, we emphasize that field potentials are distinctly informative of e-fields given their direct relation. In contrast, methods like functional magnetic resonance imaging (fMRI) infer neural processes from signals produced by numerous interlocking processes and factors, including cerebral blood flow, blood volume, and metabolic oxygenation rates, some with non-linear relations among each other (Hillman, 2014; Buxton et al., 2004; Heeger & Ress, 2002; Uludağ et al., 2004).

*LFP to neurobiology (**arrow 7**)*

The LFP can be used to draw inferences about synaptic, cellular, microcircuit, neural populations and more, because—as mentioned before—these neural structures influence the e-field, and therefore LFPs. However, because there are many ways for a circuit to create the same e-field, it depends situationally whether specific predictions can be made about neurobiological processes (Pesaran et al., 2018). To offer a few examples where they can, on the single-cell level, the LFPs index the fluctuations of intracellular membrane potential due to excitatory and inhibitory synaptic contributions, both from oscillatory (Atallah & Scanziani, 2009; Okun et al., 2010; Haider et al., 2016) and non-oscillatory regimes of activity (Chini et al., 2022; Gao et al., 2017; Lendner et al., 2023; Mazzoni et al., 2015; Trakoshis et al., 2020). On the circuit level, properties such as power in oscillatory frequency bands informs us of circuit motifs (Mendoza-Halliday et al., 2024), because different motifs robustly produce different rhythmic responses (Womelsdorf et al., 2014). Furthermore, the frequency spectra of LFPs can be informative of non-active properties of the surrounding neural tissue (Lindén et al., 2010), and the slope of the $^1/_{\text{frequency}}$ component (also known as *pink noise* or *aperiodic component*) scales with the depth of cortical layers (Halgren et al., 2021). On the population level, high-frequency activity is strongly indicative of population spiking (Ray & Maunsell, 2011), and $^1/_{\text{frequency}}$ power law exponents approximate the balance of excitatory and inhibitory synaptic drives (Gao et al., 2017; Nanda et al., 2023). This non-exhaustive list continues to grow with time. For example, recent approaches combine computational model simulations (Lindén et al., 2011; Mazzoni et al., 2015; Einevoll et al., 2013), multi-modal human brain data (Gao et al., 2020; Mahjoory et al., 2020; Markello et al., 2022), and machine learning methods (Skaar et al., 2023; Tolley et al., 2023) to establish correlations and inverse models between neural dynamics and circuit parameters.

*LFP to behavior and cognition (**arrow 8**)*

Techniques that measure local (LFP from microwire) and global potentials (EEG, MEG) have been a workhorse across paradigms in cognitive neuroscience. Here, we cover a subset of exemplifying approaches and point to more comprehensive reviews elsewhere.

As a first example, event-related potentials (ERPs) reflect the cross-trial average neural responses to internal and external events of interest. There are different kinds of ERPs, occurring at various temporal offsets and emerging from different sources in the brain (Herrera et al., 2023; Molnár, 1994). A massive body of work has shown that these patterns offer reliable signatures of behavior and internal cognitive processes, including sensory processing (Pratt, 2011), prediction error (P300; Picton, 1992; N400; Kutas & Hillyard, 1980), action planning (readiness potential; Schurger et al., 2021), attention (Luck et al., 2000), and memory (Rugg & Curran, 2007).

Second, the previously mentioned $^1/_{\mathrm{frequency}}$ component across the LFP is predictive of arousal levels (Waschke et al., 2019), sleep stages (Lendner et al., 2020), and explains variability in cognitive functions like attention (Waschke et al., 2021), memory performance (Donoghue et al., 2020; see also (Lim & Goldman, 2013), and language learning (Cross et al., 2022).

Third, research has capitalized on the full range of LFP dynamics to predict cognitive processing by searching for systematic relations between brain activity and behavior of interest in a data-driven fashion. Relevant approaches include statistical techniques like multivariate pattern analysis (MVPA; Cichy & Pantazis, 2017; Grootswagers et al., 2017; King & Dehaene, 2014; Sandhaeger & Siegel, 2023) and neural network approaches (Frey et al., 2021; Garrett et al., 2003). Besides predicting positional (Jensen & Lisman, 2000; Reifenstein et al., 2012), and bodily variables (Flint et al., 2012), these techniques confer information about internal processes that can be difficult or impossible to assess behaviorally. For example, field potentials are informative toward attentional focus (Esghaei & Daliri, 2014; Thiery et al., 2016; Tremblay et al., 2015), the contents of working memory (Polanía et al., 2015), the evolution of long-term memory processes (Kerrén et al., 2022; Linde-Domingo et al., 2019; Staresina & Wimber, 2019), mental event replay (Y. Liu et al., 2019; Michelmann et al., 2019), and internal decision-making variables (Z. Liu et al., 2022). In this way, the LFP adds to our repertoire of behavioral and cognitive measurements by shining a light on opaque internal neurocognitive processes, affording mechanistic insights hard to obtain via psychological experimentation.

5. The theoretical role of oscillations

In this section, we hone in on the phenomenon of oscillations (Figure 2). As with our previous discussion of LFP and electric fields, our aim is to clarify entangled uses of the term *oscillation*, and to foster a common ground for scientific discussion and investigation. While it is generally accepted that "oscillation" refers to a specific kind of temporal structure, the term has a multiplicity of uses across the cognitive and systems neuroscience literature. In contrast to its straightforward mathematical definition (a function $f(x)$ is oscillatory when $f(x) = f(x + T)$ for some non-zero period, T), defining oscillations is less straightforward in the biological sciences, in which nothing repeats perfectly or indefinitely. This results in two distinct ambiguities. First, the term *oscillation* is used indiscriminately to refer to a specific kind of temporal structure in measurements or in processes. Second, there is a lack of consensus on how to identify and distinguish oscillations from other dynamical features, regardless of whether that concerns measurements or processes (Bánki et al., 2022). These ambiguities feed into two further sources of disagreement in the field: 1) the degree to which oscillations in the e-field exert causal effects, and 2) the role oscillations play in neural computation.

5.1 Oscillation in measurement and process

As with the distinction between e-fields and LFP, it is crucial to distinguish oscillations in the measurements we use to study neurobiological systems from oscillations in the processes themselves:

Oscillations-in-measurements are periodic-like structures in temporally evolving signals, such as the LFP (Figure 2, top row). This includes persistent rhythms, such as the 6 to 10 Hz fluctuations observed in data from the rodent hippocampus (Vanderwolf, 1969), as well as short-lived transients

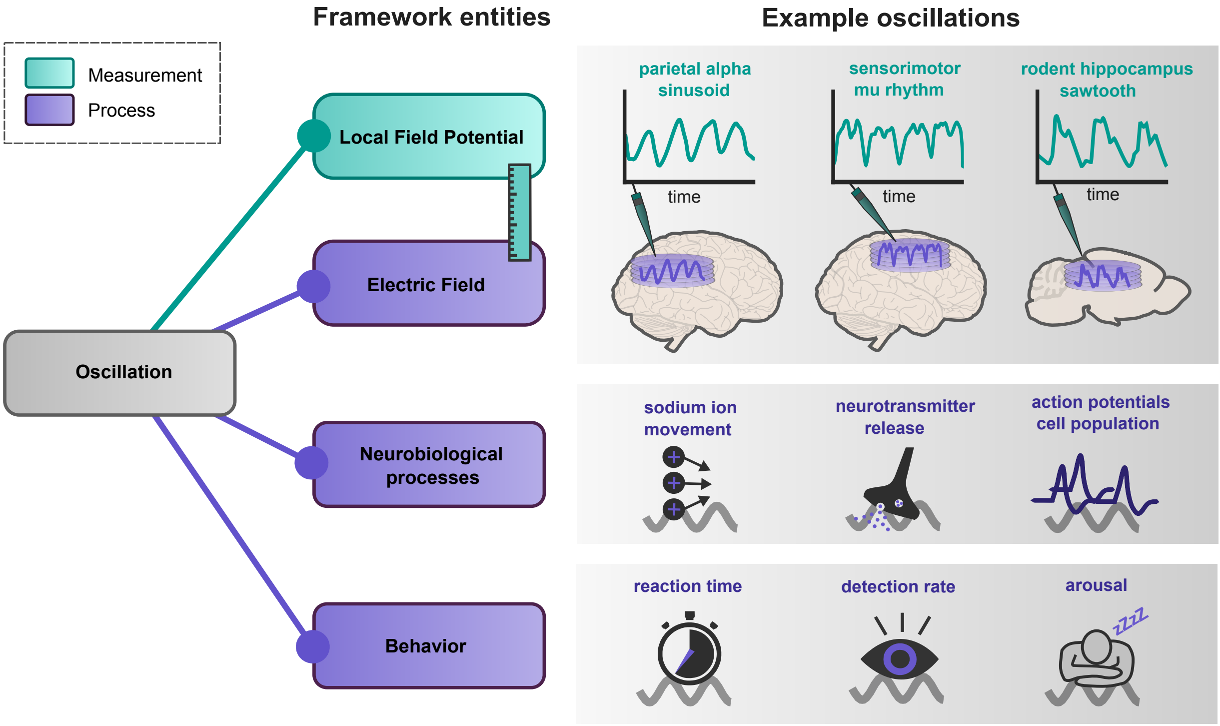

Figure 2. Oscillations in measurement and process
Oscillations are characterized by rhythmic temporal structure in any of the entities in our framework—manifesting variously in both measurements and physical processes. We outline a few example oscillations for each of our framework entities (right side). For example, rhythmic fluctuations in EEG signals, electric fields, neurotransmitter release, and detection rate each characterize one *type* of oscillation (for details, see Section 5.2).

(Jones, 2016) like the several hundred milliseconds-long bursts of 20 Hz oscillations observed in data from human primary somatosensory cortex (Shin et al., 2017). These dynamical features may or may not be visible to the naked eye, and are more commonly quantified with techniques like Fourier and wavelet transforms (Cohen, 2014), temporal filters (e.g., bandpass), and approaches that extract oscillatory components by applying linear projections to the data (Makeig et al., 1995; Parra et al., 2005; Schaworonkow & Voytek, 2021; Cohen, 2017).

In contrast, *oscillations-in-process* are typified by rhythmically repeating sequences of physical events (see Section 5.2 for demarcation criteria). In addition to electric fields, oscillations also occur in neurobiological processes such as the spiking of individual neurons (Hutcheon & Yarom, 2000; Stiefel & Ermentrout, 2016) and populations (Buzsáki & Draguhn, 2004), the opening and closing of membrane ion channels (Dorval, 2006), gene expression (Li et al., 2013), and cerebral hemodynamics and metabolism (Obrig et al., 2000), as well as in behavior (Honey et al., 2018), including memory (Ter Wal et al., 2021) and attentional processes (Fiebelkorn et al., 2013; Landau & Fries, 2012; but see Brookshire, 2022 & Vinck et al., 2022 for analytical considerations; Figure 2).

Oscillations typically emerge from the interaction of multiple connected processes, such as through the presence of negative feedback or nested loops (Strogatz, 2019). For example, networks of mutually inhibiting neurons (Matsuoka, 1985) and more complex configurations of excitatory and inhibitory neurons naturally instantiate a push-pull dynamic (Börgers & Kopell, 2008; Buzsáki & Wang, 2012; Kopell et al., 2000; Whittington et al., 2000; Womelsdorf et al., 2014) which produces interdependent rhythmic fluctuations in population spike rate, synaptic currents, and ultimately, the surrounding e-field. On the cellular level, the interplay between depolarizing and hyperpolarizing conductances produces rhythmic fluctuations in the membrane potential and spiking dynamics of individual neurons (Lopes Da Silva, 1991; Steriade & Llinás, 1988).

5.2. Inferring oscillations-in-process from oscillations-in-measurement

In most cases, we are not interested in the measurements themselves, but rather the oscillations-in-process they may reflect, and it is worth noting explicitly and exploring how one might occur without the other. Furthermore, inferring oscillations-in-process from measurements carries with it two challenges of demarcation: (1) how are oscillations-in-measurement identified among other patterns in our signals, and (2) what differentiates *any* rhythmically fluctuating process from a genuine oscillation-in-process.

The first challenge concerns the demarcation of oscillations in measurement from colored noise and other aperiodic fluctuations seen widely across neural signals (He, 2014). Moreover, oscillations may take non-sinusoidal shapes, such as a sawtooth (Cole & Voytek, 2017) or μ-like shape (Arroyo et al., 1993). All of these produce spectral power at non-fundamental frequencies, such as around harmonic frequencies (Donoghue et al., 2020; Schaworonkow, 2023). The field is actively developing techniques and guidelines to improve our signal analysis capabilities (Gross, 2014), including algorithms that factor in colored noise (Donoghue et al., 2022; Gerster et al., 2022), methods that account for the waveform shape of oscillations (Cole & Voytek, 2017; Quinn et al., 2021), quantification techniques that rely on phase consistency (Tallon-Baudry et al., 1996), and spatial filters that amplify detection of weaker rhythms (Schaworonkow & Voytek, 2021). Importantly, these points concern not only oscillations in brain activity, but apply to the detection of any oscillation from time series measurements, including oscillations in cognitive and behavioral data (Brookshire, 2022; Vinck et al., 2022).

Second, even when a reliable rhythmic pattern is detected in neural recordings, this need not always be produced by oscillations-in-process. For example, when rhythmic trains of stimuli are presented (such as a sequence of sounds), recordings of brain activity will contain a rhythmic component simply because each stimulus produces an ERP, with the concatenation of such responses giving the illusion of an oscillation (Capilla et al., 2011; Zoefel et al., 2018). However, oscillations-in-process arise from oscillators and their unique properties: oscillators have a rate at which they preferentially fluctuate (i.e., they have a natural and resonance frequency), and they operate in a self-reinforcing fashion—both of which leave their mark on electrophysiological measurements (van Bree et al., 2022; but see Doelling & Assaneo, 2021 for a critical perspective). For example, the self-reinforcing nature of oscillators means that rhythmic activity is expected to persist for one or more cycles after external inputs have ceased (van Bree et al., 2021; Kösem et al., 2018; Lakatos et al., 2013; Bouwer et al., 2023; Hanslmayr et al., 2014; Albouy et al., 2017), and the existence of preferred oscillator frequencies entails that as the distance in frequency between external rhythm and oscillator increases, more stimulus intensity is required to produce synchronization (Pikovsky et al., 2001; Henao et al., 2020). Thus, repetitions of processes are necessary but not sufficient for the presence of an oscillation-in-process. What is also necessary is the involvement of an oscillator, and our ability to evaluate if this is the case (rather than assume as much) depends on the experimental context.

The implicit conflation of *oscillations-in-process* and *oscillations-in-measurement* could contribute to disagreement about whether oscillations are epiphenomenal. Indeed, if two discussants implicitly associate the word oscillation in varying degrees with periodicity in the LFP versus periodicity in physical processes, scientific exchanges between them will be misdirected from the outset. For an overview of related ambiguities, see Box 2.

Box 2. Ambiguity of the term oscillation

After having spelled out the difference between oscillation-in-measurement and oscillation-in-process, we explore two terminological ambiguities that can occur in the literature: First, in the case of oscillation-in-process, it is not always apparent whether authors are referring to fluctuating e-fields only, or also to the entire generating mechanism associated with it (Buzsáki et al., 2004). For example, the claim that alpha oscillations underpin attention might on the one hand mean that the e-fields are doing the primary causal work (e.g., via ephaptic coupling), or on the other hand that the neurobiological events that produced the e-fields are doing the heavy lifting.

Second, at times the same terminology is used when referring to both a given oscillation-in-process as well as its corresponding oscillations-in-measurement (this differs from the previous point, which concerns processes only). For example, “theta oscillation” might refer to fluctuations in physical events in the brain *and* to fluctuations in a measured signal between 4 to 8 Hz, with the implicit (though potentially incorrect) understanding that the two entities are tightly coupled. This distinction is non-trivial, as theta-in-measurement can be explained by a plethora of other neural processes. For one, 4-8 Hz peaks in the signal might reflect e-fields from local circuit operations at a source of interest such as the hippocampus, or they might reflect volume conducted e-fields of surrounding structures such as the medial septum and olfactory bulb (Pignatelli et al., 2012; Schneider et al., 2021). Second, signal peaks might reflect different types of processes even near the source of interest, such as atropine sensitive and atropine insensitive theta (Stewart & Fox, 1989).

Putting all this together, “theta” might simultaneously refer to (1) peaks in the frequency spectrum between 4 and 8 Hz of a signal, (2) fluctuating e-fields originating from dipole sources in the hippocampus, (3) e-fields generated by axonal projection of volume conduction far away from the source, (4) the underlying circuitry necessary to produce e-fields over and above the e-fields themselves, or (5) a mix of all of the above including signal, generating mechanisms, task variables inducing the oscillation. Such ambiguity naturally leads to confusion, as well as to empirical and conceptual disagreement regarding the epiphenomenal nature of oscillations. Although this example isolates “theta” as a canonical example, it is equally applicable to the various connotations of alpha (thalamus, visual cortex, attention), beta (motor, motor cortex, basal ganglia), gamma (perception, sensory cortex, pyramidal-interneuron-gamma circuits), and other characteristic frequency bands.

5.3 The potential role of oscillatory ephaptic coupling

In section 4, we discussed evidence for the causal role of e-fields towards neurobiological processing. Here, we evaluate a variation of the ephaptic coupling hypothesis which considers *oscillating* e-fields in particular. Put differently, what causal powers might be exerted by e-fields which are fluctuating periodically at characteristic frequencies?

A fundamental insight from the physics of oscillators is that weak perturbations can produce strong and diverse effects on systems of coupled oscillators (Pikovsky et al., 2001). In the brain, cortical neurons operate at a noise-driven, high-conductance state near threshold (Destexhe et al., 2003). From this basis, weak e-fields have the potential to exert strong effects even if they cannot in isolation cause neurons to discharge action potentials. Specifically, a key idea is that oscillatory fluctuations in the e-field riding on top of background noise dynamics can translate into changes to spiking activity across masses of neurons. The prediction is that oscillations in the e-field which closely match the intrinsic or synaptically-driven oscillations in neurons can amount to an additional force on top of classical mechanisms, where the coordinated temporal summation (which is intrinsically present in waxing and waning oscillations) influences the amount of rhythmic spiking across cell populations.

Moreover, even if the e-field fluctuations are not aligned (in terms of shape, frequency, or phase) with the spectral content of neurons’ endogenous or other input dynamics, the fields might compete for control over spike timing. In indirect support of this, external fields alter the rhythmicity of neuronal spiking (Vieira et al., 2023). For example, the application of a weak electric field (~1 V/m) at 5 Hz to neurons participating in a theta oscillation reduced their synchronization to it, and stronger stimulation (~2 V/m) caused the neurons to entrain to the external rhythm instead (M. R. Krause et al., 2022).

Furthermore, even if e-fields are not oscillating, the degree of rhythmic spiking of neurons could be assisted through stochastic resonance, which is a phenomenon where weak and otherwise undetectable processes are boosted by the addition of noise (Gluckman et al., 1996; Vázquez-Rodríguez et al., 2017). Together, these findings preliminarily suggest that oscillatory e-fields are a physical process with sculpting functions, and that even non-oscillating e-fields can bolster rhythmic firing modes. With that said, the methodological considerations and caveats covered in Section 4 apply here too.

5.4 Oscillatory computation

Regardless of the causal role that e-fields play in oscillatory processes, a key question in neuroscience is what role, if any, oscillations-in-process across levels of organization play in neural computation. Under the causal stance with regard to neuronal computation, oscillations considered as an intertwined set of neurobiological processes serve an active coordinating function to information exchange across populations of neurons. Under the non-causal stance, even if oscillations reflect a mode of brain activity that correlates with cognition, oscillations are not granted processing capacities required to influence cognition. These stances subtly differ from the range of positions one might have on the causal status of e-fields. Specifically, one can coherently hold the selective view that e-fields are causally important for some homeostatic or other biological functions, while rejecting that oscillations-in-process—e-field or otherwise—play a causal role in the mechanisms of neural computations underlying cognition.

In this section, we outline a view that oscillations-in-process implement a kind of neural syntax (Buzsáki, 2019; Figure 3): an arrangement of neural activity such that it is optimally interpretable to downstream readers (Buzsáki, 2010). We argue that this syntax relies on the ability of oscillations to orchestrate neural activity in time, space, and frequency (Figure 3), endowing neural circuits capable of information processing with the ability to flexibly implement multiple functions. In the remainder of this section, we discuss each form of orchestration in turn, starting with the organization of computation through a temporal syntax.

Like the clock of a digital computer which discretizes electrical activity into functionally-related packets, oscillations are theorized to group functionally-related spikes into distinct oscillatory cycles, and/or to distinct phases within a cycle (Figure 3; left). Prominent examples include the widely observed grouping of spikes into cell assemblies by 30-100 Hz (gamma) oscillations (Lisman & Jensen, 2013; Buzsáki & Wang, 2012; Engel et al., 1991; Fries et al., 2007; Harris et al., 2003), and the sampling of possible behavioral trajectories by hippocampal theta oscillations in rodents (Kay et al., 2020; Ujfalussy & Orbán, 2022; Lisman & Redish, 2009) and humans (1-4 Hz; Qasim et al., 2021; Reddy et al., 2021), whereby spikes at early phases represent past, and those at later phases represent possible future positions of the animal, respectively. By inducing temporal synchrony, grouping-by-oscillations allows assemblies of cells to discharge downstream (e.g. postsynaptic) readers, which require multiple active presynaptic partners to induce an action potential (Liebe et al., 2022).

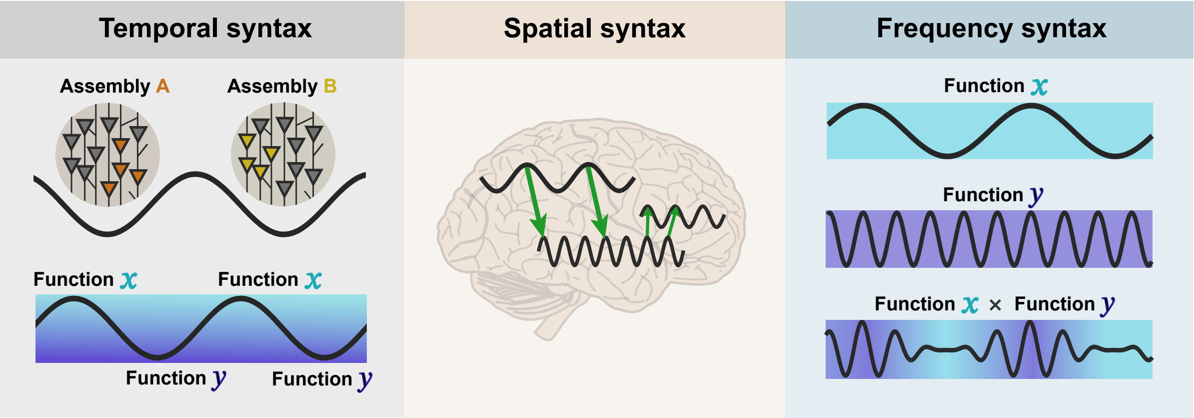

Figure 3. Oscillations as orchestrators of neural computation
Oscillations are hypothesized to systematically organize neuronal activity in time, space, and frequency. Under a temporal syntax, different computational functions are alternated in a waxing and waning fashion. Under a spatial syntax, ensembles across regions of the brain synchronize excitable phases, establishing functionally-distinct interregional communication channels. Under a frequency syntax, circuits and intracellular processes with different frequencies implement different functions.

Oscillations do not only group synchronous outputs, but they also provide windows of opportunity in which neurons are sensitive to inputs via fluctuations between hyperpolarized and depolarized phases of neuronal membrane potentials (Shewcraft et al., 2020). Then, through the coordination of synchronous and sensitive oscillatory phases between brain regions, oscillations provide a *spatial syntax* to neural computation, enabling information-coding ensembles to effectively communicate with downstream readers during systematic timeframes (Fries, 2005; Hahn et al., 2019; but see Schneider et al., 2021 for critical considerations; Figure 3; middle). For example, theta oscillations enable communication between hippocampal region CA1 and entorhinal regions via the perforant path, and from CA3 via the Schaffer collaterals at alternating phases of the theta oscillation (Fernández-Ruiz et al., 2017), and through the coordination of distinct gamma rhythms (Fernández-Ruiz et al., 2021). Furthermore, some oscillations slowly propagate across stretches of cortex, modulating spiking along the way (Muller et al., 2018). Such traveling waves change direction when the brain moves between encoding and recall states (Mohan et al., 2024), streamlining with the notion that oscillations aid interregional information exchange.

Finally, oscillations coordinate neural processing via a *frequency syntax*, by which oscillations at different frequency bands carry functionally distinct information or perform separate computations (Figure 3; right). For example, in the rodent basal forebrain, oscillations at 20 to 35 Hz (beta), 45 to 65 Hz (gamma), and 80 to 150 Hz (high gamma) are each seen at distinct cognitive processing stages in a spatial orientation task (Tingley et al., 2018), top-down vs bottom-up signals in the neocortex are processed locally at different frequency ranges (Bastos et al., 2015; Zheng & Colgin, 2015), and high-frequency regular "burst" spiking is associated with synaptic plasticity (Friedenberger et al., 2023; Payeur et al., 2021). Oscillations at varying frequencies can use cross-frequency coupling to implement a nested frequency syntax, such as when the amplitude of fast oscillations varies along the phase of slow oscillations to encode perceptual (Canolty & Knight, 2010), memory (Bahramisharif et al., 2018; Heusser et al., 2016), or linguistic content (Murphy, 2024).

Together, we propose that oscillations are best thought of as enabling functional multiplexing: the ability of the same neural tissue to perform multiple, state-dependent functions as required depending on the context. Each kind of syntax allows neural populations to process functionally distinct signals. In short, we hypothesize that oscillations-in-process generally are central to the organization of information processing within and across networks in the brain. Finally, a nascent question is how these ideas cohere with manifold perspectives (Box 3).

Box 3. Limit cycles and oscillatory computation

Recent theories of population coding posit that task-relevant activity emerging from large groups of neurons undergoes stereotypic patterns that are captured by movement along a manifold in lower-dimension projections of the data (Barack & Krakauer, 2021; Langdon et al., 2023). In these subspaces, we can detect motifs of aggregate brain activity that reliably underpin computation, which might take the shape of nonlinear surfaces or point or line attractors (Vyas et al., 2020). Importantly, limit cycles are a type of periodic attractor that emerges from (or can be reconstructed from) periodic and sequentially activated neuronal population, such as during repeating phase-locked firing patterns clocked by theta oscillations associated with sequential memory activation in humans (Liebe et al., 2022) and computational models (Pals et al., 2024).

Importantly however, while frequently observed rotational dynamics such as ones detected in the motor cortex (Churchland et al., 2012; Russo et al., 2018) and spinal cord (Lindén et al., 2022) are limit cycles in state space, they do not necessarily imply the existence of an oscillation-in-process. Rotational dynamics can be explained by the sequential activation of populations alone (Lebedev et al., 2019), and periodically repeating motifs can be induced by repetitive, stereotyped muscle contraction (Lindén et al., 2022). Such repeating activity is not a genuine oscillation, but more akin to our previous example of stimulus trains in auditory entrainment studies producing a concatenation of ERPs. In other words, oscillations can imply the existence of rotational dynamics along limit cycles, but rotational dynamics alone do not prove oscillations-in-process. Future experimental, modeling, and conceptual efforts are needed to establish how the oscillatory computation and manifold perspective tie together.

6. Discussion

Oscillations, local field potentials, and other key terms in the electrophysiologist's dictionary are used in various senses across the literature. Some variability might be healthy to foster pluralism, but too much divergence risks a conceptual quagmire where scientists, research groups, and subfields start to talk past each other. For example, if one party conceives of LFPs as electric fields generated locally in confined circuits, while another views LFPs as an underdetermined signal with unboundedly many processes underpinning it, then disputes on the relevance of LFPs or what research avenues are worth pursuing become misdirected from the outset. In a similar vein, the claim that oscillations are epiphenomenal leaves open (1) whether this concerns oscillations as processes, signals, or both, (2) what oscillations are epiphenomenal *toward*, (3) whether oscillations are informative in spite of their causal inefficaciousness, (4) and if so, toward which other processes they are informative or not.

In this contribution, we argue that neuroscience benefits from distinguishing measurements and processes on the one hand, and informativeness and causality on the other. We submit that these axes of analysis help us wade through terminological vagueness and orient debates toward experimental validation. Adopting this lens, we offer empirically driven answers on the casual and inferential role of processes and measurements in electrophysiology. Our answers are as follows.

First, local field potentials are measurements that reveal direct information about electric fields, as well as indirect information about neurobiological processes, cognition, and behavior. Many of these processes have causal relations between each other, though the evidence varies on a case-by-case basis. Perhaps most centrally, we argue that electric fields likely influence neuronal processing over and above being produced by it through the process of ephaptic coupling. Furthermore, we posit that oscillations are best cast as a separate entity that can arise in processes and measurements. In this context, oscillations in processes across levels of scale appear to introduce a neural syntax by which multiplexed computation is enabled. However, not all measured neural activity is oscillatory, nor does the presence of an oscillation in one entity necessitate oscillations in the other, meaning it is instructive to clarify *what* is oscillating when referring to neural processes or signals.

Finally, the outlined framework can also be applied to other neural signals and processes. For example, spikes are sometimes viewed as explanatorily superior to LFPs and oscillations, but this entity deserves its own treatment. In some contexts, the term spike refers to a signal (sharp high-frequency LFP components), and in others it refers to a neurobiological process (inter-neuronal communication over synapses; the action potential). Their relation is taken at face value, but analytical challenges emerge as they do in the inference from (oscillating) LFP to (oscillating) electric field. For example, it is challenging to consistently assign spike waveforms to physical processes in isolatable neurons. Indeed, spike sorting algorithms perform far from perfect on benchmark tests (Magland et al., 2020; Barnett et al., 2016) a problem that intensifies with the advent of high-density techniques. And with the claim that spikes are causal and informative, it again needs to be specified what it is causal and informative towards, and how much primacy it has over other measurements and processes.

Overall, the answers obtained from our reframed questions energize research programmes that tentatively consider electric fields and oscillations within them as active causal phenomena. Furthermore, even to the extent these processes are not causally relevant, their measurements yield information about behavior, cognition, as well as other dimensions relevant across the systems and cognitive neurosciences.

Acknowledgements

We thank Earl Miller for his comments on this manuscript. We also thank Roby Duncan, Erik Petersen, and members of the Voytek lab for discussions that inspired an earlier version of this work while RG was at the University of California. In addition, we thank Maria Wimber, Simon Hanslmayr, and members of their respective labs for relevant discussions while SvB was at the University of Glasgow. DL is supported by the FRQNT Strategic Clusters Program 2020-RS4-265502 - Centre UNIQUE - Union Neurosciences & Artificial Intelligence - Quebec) and the Richard and Edith Strauss Postdoctoral Fellowship in Medicine. RG is supported by the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No. 101030918 (AutoMIND).

References

Albouy, P., Weiss, A., Baillet, S., & Zatorre, R. J. (2017). Selective Entrainment of Theta Oscillations in the Dorsal Stream Causally Enhances Auditory Working Memory Performance. *Neuron*, *94*(1), 193-206.e5. https://doi.org/10.1016/j.neuron.2017.03.015

Alekseichuk, I., Wischnewski, M., & Opitz, A. (2022). A minimum effective dose for (transcranial) alternating current stimulation. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation*, *15*(5), 1221–1222. https://doi.org/10.1016/j.brs.2022.08.018

Ali, M. M., Sellers, K. K., & Frohlich, F. (2013). Transcranial Alternating Current Stimulation Modulates Large-Scale Cortical Network Activity by Network Resonance. *Journal of Neuroscience*, *33*(27), 11262–11275. https://doi.org/10.1523/JNEUROSCI.5867-12.2013

Anastassiou, C. A., Perin, R., Markram, H., & Koch, C. (2011). Ephaptic coupling of cortical neurons. *Nature Neuroscience*, *14*(2), Article 2. https://doi.org/10.1038/nn.2727

Arroyo, S., Lesser, R. P., Gordon, B., Uematsu, S., Jackson, D., & Webber, R. (1993). Functional significance of the mu rhythm of human cortex: An electrophysiologic study with subdural electrodes. *Electroencephalography and Clinical Neurophysiology*, *87*(3), 76–87. https://doi.org/10.1016/0013-4694(93)90114-B

Atallah, B. V., & Scanziani, M. (2009). Instantaneous modulation of gamma oscillation frequency by balancing excitation with inhibition. *Neuron*, *62*(4), 566–577. https://doi.org/10.1016/j.neuron.2009.04.027

Bahmani, Z., Daliri, M. R., Merrikhi, Y., Clark, K., & Noudoost, B. (2018). Working Memory Enhances Cortical Representations via Spatially Specific Coordination of Spike Times. *Neuron*, *97*(4), 967-979.e6. https://doi.org/10.1016/j.neuron.2018.01.012

Bahramisharif, A., Jensen, O., Jacobs, J., & Lisman, J. (2018). Serial representation of items during working memory maintenance at letter-selective cortical sites. *PLoS Biology*, *16*(8), e2003805. https://doi.org/10.1371/journal.pbio.2003805

Bánki, A., Brzozowska, A., Hoehl, S., & Köster, M. (2022). Neural Entrainment vs. Stimulus-Tracking: A Conceptual Challenge for Rhythmic Perceptual Stimulation in Developmental Neuroscience. *Frontiers in Psychology*, *13*, 878984. https://doi.org/10.3389/fpsyg.2022.878984

Barack, D. L., & Krakauer, J. W. (2021). Two views on the cognitive brain. *Nature Reviews Neuroscience*, *22*(6), Article 6. https://doi.org/10.1038/s41583-021-00448-6

Barack, D. L., Miller, E. K., Moore, C. I., Packer, A. M., Pessoa, L., Ross, L. N., & Rust, N. C. (2022). A call for more clarity around causality in neuroscience. *Trends in Neurosciences*, *45*(9), 654–655. https://doi.org/10.1016/j.tins.2022.06.003

Bassett, D. S., & Sporns, O. (2017). Network neuroscience. *Nature Neuroscience*, *20*(3), 353–364. https://doi.org/10.1038/nn.4502

Bastos, A. M., Loonis, R., Kornblith, S., Lundqvist, M., & Miller, E. K. (2018). Laminar recordings in frontal cortex suggest distinct layers for maintenance and control of working memory. *Proceedings of the National Academy of Sciences*, *115*(5), 1117–1122. https://doi.org/10.1073/pnas.1710323115

Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R., De Weerd, P., Kennedy, H., & Fries, P. (2015). Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels. *Neuron*, *85*(2), 390–401. https://doi.org/10.1016/j.neuron.2014.12.018

Bédard, C., Kröger, H., & Destexhe, A. (2006). Does the 1/f frequency scaling of brain signals reflect self-organized critical states? *Physical Review Letters*, *97*(11), 118102. https://doi.org/10.1103/PhysRevLett.97.118102

Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, *87*(1), 527–570. https://doi.org/10.1007/BF01797193

Bergmann, T. O., & Hartwigsen, G. (2021). Inferring Causality from Noninvasive Brain Stimulation in Cognitive Neuroscience. *Journal of Cognitive Neuroscience*, *33*(2), 195–225. https://doi.org/10.1162/jocn_a_01591

Bokil, H., Laaris, N., Blinder, K., Ennis, M., & Keller, A. (2001). Ephaptic interactions in the mammalian olfactory system. *The Journal of Neuroscience*, *21*(20), RC173.

Börgers, C., & Kopell, N. J. (2008). Gamma oscillations and stimulus selection. *Neural Computation*, *20*(2), 383–414. https://doi.org/10.1162/neco.2007.07-06-289

Bouwer, F. L., Fahrenfort, J. J., Millard, S. K., Kloosterman, N. A., & Slagter, H. A. (2023). A Silent Disco: Differential Effects of Beat-based and Pattern-based Temporal Expectations on Persistent Entrainment of Low-frequency Neural Oscillations. *Journal of Cognitive Neuroscience*, *35*(6), 990–1020. https://doi.org/10.1162/jocn_a_01985

Brookshire, G. (2022). Putative rhythms in attentional switching can be explained by aperiodic temporal structure. *Nature Human Behaviour*, *6*(9), 1280–1291. https://doi.org/10.1038/s41562-022-01364-0

Buxton, R. B., Uludağ, K., Dubowitz, D. J., & Liu, T. T. (2004). Modeling the hemodynamic response to brain activation. *NeuroImage*, *23 Suppl 1*, S220-233. https://doi.org/10.1016/j.neuroimage.2004.07.013

Buzsáki, G. (2010). Neural syntax: Cell assemblies, synapsembles and readers. *Neuron*, *68*(3), 362–385. https://doi.org/10.1016/j.neuron.2010.09.023

Buzsáki, G. (2019). Brain Rhythms Provide a Framework for Neural Syntax. In G. Buzsáki (Ed.), *The Brain from Inside Out* (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780190905385.003.0006

Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents—EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, *13*(6), Article 6. https://doi.org/10.1038/nrn3241

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

Buzsáki, G., Geisler, C., Henze, D. A., & Wang, X.-J. (2004). Interneuron Diversity series: Circuit complexity and axon wiring economy of cortical interneurons. *Trends in Neurosciences*, *27*(4), 186–193. https://doi.org/10.1016/j.tins.2004.02.007

Buzsáki, G., & Wang, X.-J. (2012). Mechanisms of Gamma Oscillations. *Annual Review of Neuroscience*, *35*(1), 203–225. https://doi.org/10.1146/annurev-neuro-062111-150444

Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences*, *14*(11), 506–515. https://doi.org/10.1016/j.tics.2010.09.001

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), e14543.

Chan, C. Y., Hounsgaard, J., & Nicholson, C. (1988). Effects of electric fields on transmembrane potential and excitability of turtle cerebellar Purkinje cells in vitro. *The Journal of Physiology*, *402*(1), 751–771. https://doi.org/10.1113/jphysiol.1988.sp017232

Chen, Y., Dhamala, M., Bollimunta, A., Schroeder, C. E., & Ding, M. (2011). Current Source Density Analysis of Ongoing Neural Activity: Theory and Application. In R. P. Vertes & R. W. Stackman (Eds.), *Electrophysiological Recording Techniques* (Vol. 54, pp. 27–40). Humana Press. https://doi.org/10.1007/978-1-60327-202-5_2

Chini, M., Pfeffer, T., & Hanganu-Opatz, I. (2022). An increase of inhibition drives the developmental decorrelation of neural activity. *eLife*, *11*, e78811. https://doi.org/10.7554/eLife.78811

Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Foster, J. D., Nuyujukian, P., Ryu, S. I., & Shenoy, K. V. (2012). Neural population dynamics during reaching. *Nature*, *487*(7405), Article 7405. https://doi.org/10.1038/nature11129

Cichy, R. M., & Pantazis, D. (2017). Multivariate pattern analysis of MEG and EEG: A comparison of representational structure in time and space. *NeuroImage*, *158*, 441–454. https://doi.org/10.1016/j.neuroimage.2017.07.023

Clayton, M. S., Yeung, N., & Kadosh, R. C. (2015). The roles of cortical oscillations in sustained attention. *Trends in Cognitive Sciences*, *19*(4), 188–195. https://doi.org/10.1016/j.tics.2015.02.004

Cohen, M. X. (2014). *Analyzing Neural Time Series Data: Theory and Practice*. The MIT Press. https://doi.org/10.7551/mitpress/9609.001.0001

Cohen, M. X. (2017). Multivariate cross-frequency coupling via generalized eigendecomposition. *eLife*, *6*, e21792. https://doi.org/10.7554/eLife.21792

Cole, & Voytek. (2017). Brain oscillations and the importance of waveform shape. *Trends Cogn. Sci.*, *21*. https://doi.org/10.1016/j.tics.2016.12.008

Cross, Z. R., Corcoran, A. W., Schlesewsky, M., Kohler, M. J., & Bornkessel-Schlesewsky, I. (2022). Oscillatory and Aperiodic Neural Activity Jointly Predict Language Learning. *Journal of Cognitive Neuroscience*, *34*(9), 1630–1649. https://doi.org/10.1162/jocn_a_01878

Deng, Y., Reinhart, R. M., Choi, I., & Shinn-Cunningham, B. G. (2019). Causal links between parietal alpha activity and spatial auditory attention. *eLife*, *8*, e51184. https://doi.org/10.7554/eLife.51184

Destexhe, A., Rudolph, M., & Paré, D. (2003). The high-conductance state of neocortical neurons in vivo. *Nature Reviews Neuroscience*, *4*(9), Article 9. https://doi.org/10.1038/nrn1198

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.

Donoghue, T., Haller, M., Peterson, E. J., Varma, P., Sebastian, P., Gao, R., Noto, T., Lara, A. H., Wallis, J. D., Knight, R. T., Shestyuk, A., & Voytek, B. (2020). Parameterizing neural power spectra into periodic and aperiodic components. *Nature Neuroscience*, *23*(12), 1655–1665. https://doi.org/10.1038/s41593-020-00744-x

Donoghue, T., Schaworonkow, N., & Voytek, B. (2022). Methodological considerations for studying neural oscillations. *European Journal of Neuroscience*, *55*(11–12), 3502–3527. https://doi.org/10.1111/ejn.15361

Dorval, A. D. (2006). The Rhythmic Consequences of Ion Channel Stochasticity. *The Neuroscientist*, *12*(5), 442–448. https://doi.org/10.1177/1073858406290793

Einevoll, G. T., Kayser, C., Logothetis, N. K., & Panzeri, S. (2013). Modelling and analysis of local field potentials for studying the function of cortical circuits. *Nature Reviews Neuroscience*, *14*(11), Article 11. https://doi.org/10.1038/nrn3599

Engel, A. K., Kreiter, A. K., König, P., & Singer, W. (1991). Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. *Proceedings of the National Academy of Sciences of the United States of America*, *88*(14), 6048–6052. https://doi.org/10.1073/pnas.88.14.6048

Esghaei, M., & Daliri, M. R. (2014). Decoding of Visual Attention from LFP Signals of Macaque MT. *PLOS ONE*, *9*(6), e100381. https://doi.org/10.1371/journal.pone.0100381

Fernández-Ruiz, A., Oliva, A., Nagy, G. A., Maurer, A. P., Berényi, A., & Buzsáki, G. (2017). Entorhinal-CA3 Dual-Input Control of Spike Timing in the Hippocampus by Theta-Gamma Coupling. *Neuron*, *93*(5), 1213-1226.e5. https://doi.org/10.1016/j.neuron.2017.02.017

Fernández-Ruiz, A., Oliva, A., Soula, M., Rocha-Almeida, F., Nagy, G. A., Martin-Vazquez, G., & Buzsáki, G. (2021). Gamma rhythm communication between entorhinal cortex and dentate gyrus neuronal assemblies. *Science*, *372*(6537), eabf3119. https://doi.org/10.1126/science.abf3119

Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic Sampling within and between Objects despite Sustained Attention at a Cued Location. *Current Biology*, *23*(24), 2553–2558. https://doi.org/10.1016/j.cub.2013.10.063

Flint, R. D., Lindberg, E. W., Jordan, L. R., Miller, L. E., & Slutzky, M. W. (2012). Accurate decoding of reaching movements from field potentials in the absence of spikes. *Journal of Neural Engineering*, *9*(4), 046006. https://doi.org/10.1088/1741-2560/9/4/046006

Francis, J. T., Gluckman, B. J., & Schiff, S. J. (2003). Sensitivity of neurons to weak electric fields. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *23*(19), 7255–7261. https://doi.org/10.1523/JNEUROSCI.23-19-07255.2003

Frey, M., Tanni, S., Perrodin, C., O'Leary, A., Nau, M., Kelly, J., Banino, A., Bendor, D., Lefort, J., Doeller, C. F., & Barry, C. (2021). Interpreting wide-band neural activity using convolutional neural networks. *eLife*, *10*, e66551. https://doi.org/10.7554/eLife.66551

Friedenberger, Z., Harkin, E., Tóth, K., & Naud, R. (2023). Silences, spikes and bursts: Three-part knot of the neural code. *The Journal of Physiology*, *601*(23), 5165–5193. https://doi.org/10.1113/JP281510

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480. https://doi.org/10.1016/j.tics.2005.08.011

Fries, P., Nikolić, D., & Singer, W. (2007). The gamma cycle. *Trends in Neurosciences*, *30*(7), 309–316. https://doi.org/10.1016/j.tins.2007.05.005

Fröhlich, F., & McCormick, D. A. (2010). Endogenous Electric Fields May Guide Neocortical Network Activity. *Neuron*, *67*(1), 129–143. https://doi.org/10.1016/j.neuron.2010.06.005

Gao, R., Peterson, E. J., & Voytek, B. (2017). Inferring synaptic excitation/inhibition balance from field potentials. *NeuroImage*, *158*, 70–78. https://doi.org/10.1016/j.neuroimage.2017.06.078

Gao, R., van den Brink, R. L., Pfeffer, T., & Voytek, B. (2020). Neuronal timescales are functionally dynamic and shaped by cortical microarchitecture. *eLife*, *9*, e61277. https://doi.org/10.7554/eLife.61277

Garrett, D., Peterson, D. A., Anderson, C. W., & Thaut, M. H. (2003). Comparison of linear, nonlinear, and feature selection methods for EEG signal classification. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, *11*(2), 141–144. https://doi.org/10.1109/TNSRE.2003.814441

Gerster, M., Waterstraat, G., Litvak, V., Lehnertz, K., Schnitzler, A., Florin, E., Curio, G., & Nikulin, V. (2022). Separating Neural Oscillations from Aperiodic 1/f Activity: Challenges and Recommendations. *Neuroinformatics*, *20*(4), 991–1012. https://doi.org/10.1007/s12021-022-09581-8

Gluckman, B. J., Netoff, T. I., Neel, E. J., Ditto, W. L., Spano, M. L., & Schiff, S. J. (1996). Stochastic Resonance in a Neuronal Network from Mammalian Brain. *Physical Review Letters*, *77*(19), 4098–4101. https://doi.org/10.1103/PhysRevLett.77.4098

Grootswagers, T., Wardle, S. G., & Carlson, T. A. (2017). Decoding Dynamic Brain Patterns from Evoked Responses: A Tutorial on Multivariate Pattern Analysis Applied to Time Series Neuroimaging Data. *Journal of Cognitive Neuroscience*, *29*(4), 677–697. https://doi.org/10.1162/jocn_a_01068

Gross, J. (2014). Analytical methods and experimental approaches for electrophysiological studies of brain oscillations. *Journal of Neuroscience Methods*, *228*, 57–66. https://doi.org/10.1016/j.jneumeth.2014.03.007

Hahn, G., Ponce-Alvarez, A., Deco, G., Aertsen, A., & Kumar, A. (2019). Portraits of communication in neuronal networks. *Nature Reviews Neuroscience*, *20*(2), 117–127. https://doi.org/10.1038/s41583-018-0094-0

Haider, B., Schulz, D. P. A., Häusser, M., & Carandini, M. (2016). Millisecond Coupling of Local Field Potentials to Synaptic Currents in the Awake Visual Cortex. *Neuron*, *90*(1), 35–42. https://doi.org/10.1016/j.neuron.2016.02.034

Halgren, M., Kang, R., Voytek, B., Ulbert, I., Fabo, D., Eross, L., Wittner, L., Madsen, J., Doyle, W. K., Devinsky, O., Halgren, E., Harnett, M. T., & Cash, S. S. (2021). *The timescale and magnitude of 1/f aperiodic activity decrease with cortical depth in humans, macaques, and mice* (p. 2021.07.28.454235). bioRxiv. https://doi.org/10.1101/2021.07.28.454235

Hanslmayr, S., Axmacher, N., & Inman, C. S. (2019). Modulating Human Memory via Entrainment of Brain Oscillations. *Trends in Neurosciences*, *42*(7), 485–499. https://doi.org/10.1016/j.tins.2019.04.004

Hanslmayr, S., Matuschek, J., & Fellner, M.-C. (2014). Entrainment of Prefrontal Beta Oscillations Induces an Endogenous Echo and Impairs Memory Formation. *Current Biology*, *24*(8), 904–909. https://doi.org/10.1016/j.cub.2014.03.007

Harris, K. D., Csicsvari, J., Hirase, H., Dragoi, G., & Buzsáki, G. (2003). Organization of cell assemblies in the hippocampus. *Nature*, *424*(6948), 552–556. https://doi.org/10.1038/nature01834

He, B. J. (2014). Scale-free brain activity: Past, present, and future. *Trends in Cognitive Sciences*, *18*(9), 480–487. https://doi.org/10.1016/j.tics.2014.04.003

Heeger, D. J., & Ress, D. (2002). What does fMRI tell us about neuronal activity? *Nature Reviews Neuroscience*, *3*(2), Article 2. https://doi.org/10.1038/nrn730

Henao, D., Navarrete, M., Valderrama, M., & Le Van Quyen, M. (2020). Entrainment and synchronization of brain oscillations to auditory stimulations. *Neuroscience Research*, *156*, 271–278. https://doi.org/10.1016/j.neures.2020.03.004

Herrera, B., Sajad, A., Errington, S. P., Schall, J. D., & Riera, J. J. (2023). Cortical origin of theta error signals. *Cerebral Cortex*, *33*(23), 11300–11319. https://doi.org/10.1093/cercor/bhad367

Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta Oscillations in Human Memory. *Trends in Cognitive Sciences*, *24*(3), 208–227. https://doi.org/10.1016/j.tics.2019.12.006

Hesp, C. (2021). Beyond connectionism: A neuronal dance of ephaptic and synaptic interactions. *Physics of Life Reviews*, *36*, 40–43. https://doi.org/10.1016/j.plrev.2020.08.002

Heusser, A. C., Poeppel, D., Ezzyat, Y., & Davachi, L. (2016). Episodic sequence memory is supported by a theta–gamma phase code. *Nature Neuroscience*, *19*(10), Article 10. https://doi.org/10.1038/nn.4374

Hillman, E. M. C. (2014). Coupling Mechanism and Significance of the BOLD Signal: A Status Report. *Annual Review of Neuroscience*, *37*, 161–181. https://doi.org/10.1146/annurev-neuro-071013-014111

Honey, C. J., Newman, E. L., & Schapiro, A. C. (2018). Switching between internal and external modes: A multiscale learning principle. *Network Neuroscience (Cambridge, Mass.)*, *1*(4), 339–356. https://doi.org/10.1162/NETN_a_00024

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

Jefferys, J. G. (1995). Nonsynaptic modulation of neuronal activity in the brain: Electric currents and extracellular ions. *Physiological Reviews*, *75*(4), 689–723.

Jensen, O., & Lisman, J. (2000). Position Reconstruction From an Ensemble of Hippocampal Place Cells: Contribution of Theta Phase Coding. *Journal of Neurophysiology*, *83*(5), 2602–2609. https://doi.org/10.1152/jn.2000.83.5.2602

Johnson, L., Alekseichuk, I., Krieg, J., Doyle, A., Yu, Y., Vitek, J., Johnson, M., & Opitz, A. (2020). Dose-dependent effects of transcranial alternating current stimulation on spike timing in awake nonhuman primates. *Science Advances*, *6*(36), eaaz2747. https://doi.org/10.1126/sciadv.aaz2747

Jones, S. R. (2016). When brain rhythms aren't 'rhythmic': Implication for their mechanisms and meaning. *Current Opinion in Neurobiology*, *40*, 72–80. https://doi.org/10.1016/j.conb.2016.06.010

Kay, K., Chung, J. E., Sosa, M., Schor, J. S., Karlsson, M. P., Larkin, M. C., Liu, D. F., & Frank, L. M. (2020). Constant Sub-second Cycling between Representations of Possible Futures in the Hippocampus. *Cell*, *180*(3), 552-567.e25. https://doi.org/10.1016/j.cell.2020.01.014

Kerrén, C., van Bree, S., Griffiths, B. J., & Wimber, M. (2022). Phase separation of competing memories along the human hippocampal theta rhythm. *eLife*, *11*, e80633. https://doi.org/10.7554/eLife.80633

Khanna, P., & Carmena, J. M. (2015). Neural oscillations: Beta band activity across motor networks. *Current Opinion in Neurobiology*, *32*, 60–67. https://doi.org/10.1016/j.conb.2014.11.010

King, J.-R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: The temporal generalization method. *Trends in Cognitive Sciences*, *18*(4), 203–210. https://doi.org/10.1016/j.tics.2014.01.002

Kopell, N., Ermentrout, G. B., Whittington, M. A., & Traub, R. D. (2000). Gamma rhythms and beta rhythms have different synchronization properties. *Proceedings of the National Academy of Sciences*, *97*(4), 1867–1872. https://doi.org/10.1073/pnas.97.4.1867

Kösem, A., Bosker, H. R., Takashima, A., Meyer, A., Jensen, O., & Hagoort, P. (2018). Neural Entrainment Determines the Words We Hear. *Current Biology*, *28*(18), 2867-2875.e3. https://doi.org/10.1016/j.cub.2018.07.023

Krahe, R., & Gabbiani, F. (2004). Burst firing in sensory systems. *Nature Reviews Neuroscience*, *5*(1), 13–23. https://doi.org/10.1038/nrn1296

Krause, M. R., Vieira, P. G., Csorba, B. A., Pilly, P. K., & Pack, C. C. (2019). Transcranial alternating current stimulation entrains single-neuron activity in the primate brain. *Proceedings of the National Academy of Sciences*, *116*(12), 5747–5755. https://doi.org/10.1073/pnas.1815958116

Krause, M. R., Vieira, P. G., Thivierge, J.-P., & Pack, C. C. (2022). Brain stimulation competes with ongoing oscillations for control of spike timing in the primate brain. *PLOS Biology*, *20*(5), e3001650. https://doi.org/10.1371/journal.pbio.3001650

Krause, M. R., Zanos, T. P., Csorba, B. A., Pilly, P. K., Choe, J., Phillips, M. E., Datta, A., & Pack, C. C. (2017). Transcranial Direct Current Stimulation Facilitates Associative Learning and Alters Functional Connectivity in the Primate Brain. *Current Biology*, *27*(20), 3086-3096.e3. https://doi.org/10.1016/j.cub.2017.09.020

Krause, V., Meier, A., Dinkelbach, L., & Pollok, B. (2016). Beta Band Transcranial Alternating (tACS) and Direct Current Stimulation (tDCS) Applied After Initial Learning Facilitate Retrieval of a Motor Sequence. *Frontiers in Behavioral Neuroscience*, *10*, 4. https://doi.org/10.3389/fnbeh.2016.00004

Kutas, M., & Hillyard, S. A. (1980). Reading Senseless Sentences: Brain Potentials Reflect Semantic Incongruity. *Science*, *207*(4427), 203–205. https://doi.org/10.1126/science.7350657

Lakatos, P., Musacchia, G., O'Connel, M. N., Falchier, A. Y., Javitt, D. C., & Schroeder, C. E. (2013). The Spectrotemporal Filter Mechanism of Auditory Selective Attention. *Neuron*, *77*(4), 750–761. https://doi.org/10.1016/j.neuron.2012.11.034

Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology: CB*, *22*(11), 1000–1004. https://doi.org/10.1016/j.cub.2012.03.054

Langdon, C., Genkin, M., & Engel, T. A. (2023). A unifying perspective on neural manifolds and circuits for cognition. *Nature Reviews Neuroscience*, *24*(6), Article 6. https://doi.org/10.1038/s41583-023-00693-x

Lebedev, M. A., Ossadtchi, A., Mill, N. A., Urpí, N. A., Cervera, M. R., & Nicolelis, M. A. L. (2019). Analysis of neuronal ensemble activity reveals the pitfalls and shortcomings of rotation dynamics. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-54760-4

Lendner, J. D., Helfrich, R. F., Mander, B. A., Romundstad, L., Lin, J. J., Walker, M. P., Larsson, P. G., & Knight, R. T. (2020). An electrophysiological marker of arousal level in humans. *eLife*, *9*, e55092. https://doi.org/10.7554/eLife.55092

Lendner, J. D., Niethard, N., Mander, B. A., van Schalkwijk, F. J., Schuh-Hofer, S., Schmidt, H., Knight, R. T., Born, J., Walker, M. P., Lin, J. J., & Helfrich, R. F. (2023). Human REM sleep recalibrates neural activity in support of memory formation. *Science Advances*, *9*(34), eadj1895. https://doi.org/10.1126/sciadv.adj1895

Levin, M. (2012). Molecular bioelectricity in developmental biology: New tools and recent discoveries: Control of cell behavior and pattern formation by transmembrane potential gradients. *BioEssays*, *34*(3), 205–217. https://doi.org/10.1002/bies.201100136

Levin, M. (2014). Molecular bioelectricity: How endogenous voltage potentials control cell behavior and instruct pattern regulation in vivo. *Molecular Biology of the Cell*, *25*(24), 3835–3850. https://doi.org/10.1091/mbc.E13-12-0708

Li, J. Z., Bunney, B. G., Meng, F., Hagenauer, M. H., Walsh, D. M., Vawter, M. P., Evans, S. J., Choudary, P. V., Cartagena, P., Barchas, J. D., Schatzberg, A. F., Jones, E. G., Myers, R. M., Watson, S. J., Akil, H., & Bunney, W. E. (2013). Circadian patterns of gene expression in the human brain and disruption in major depressive disorder. *Proceedings of the National Academy of Sciences*, *110*(24), 9950–9955. https://doi.org/10.1073/pnas.1305814110

Liebe, S., Niediek, J., Pals, M., Reber, T. P., Faber, J., Bostroem, J., Elger, C. E., Macke, J. H., & Mormann, F. (2022). *Phase of firing does not reflect temporal order in sequence memory of humans and recurrent neural networks* [Preprint]. Neuroscience. https://doi.org/10.1101/2022.09.25.509370

Lim, S., & Goldman, M. S. (2013). Balanced cortical microcircuitry for maintaining information in working memory. *Nature Neuroscience*, *16*(9), 1306–1314. https://doi.org/10.1038/nn.3492

Linde-Domingo, J., Treder, M. S., Kerrén, C., & Wimber, M. (2019). Evidence that neural information flow is reversed between object perception and object reconstruction from memory. *Nature Communications*, *10*(1), 179. https://doi.org/10.1038/s41467-018-08080-2

Lindén, H., Petersen, P. C., Vestergaard, M., & Berg, R. W. (2022). Movement is governed by rotational neural dynamics in spinal motor networks. *Nature*, *610*(7932), 526–531. https://doi.org/10.1038/s41586-022-05293-w

Lindén, H., Pettersen, K. H., & Einevoll, G. T. (2010). Intrinsic dendritic filtering gives low-pass power spectra of local field potentials. *Journal of Computational Neuroscience*, *29*(3), 423–444. https://doi.org/10.1007/s10827-010-0245-4

Lindén, H., Tetzlaff, T., Potjans, T. C., Pettersen, K. H., Grün, S., Diesmann, M., & Einevoll, G. T. (2011). Modeling the Spatial Reach of the LFP. *Neuron*, *72*(5), 859–872. https://doi.org/10.1016/j.neuron.2011.11.006

Lisman, J., & Jensen, O. (2013). The θ-γ neural code. *Neuron*, *77*(6), 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007

Lisman, J., & Redish, A. D. (2009). Prediction, sequences and the hippocampus. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1521), 1193–1201. https://doi.org/10.1098/rstb.2008.0316

Liu, Y., Dolan, R. J., Kurth-Nelson, Z., & Behrens, T. E. J. (2019). Human Replay Spontaneously Reorganizes Experience. *Cell*, *178*(3), 640-652.e14. https://doi.org/10.1016/j.cell.2019.06.012

Liu, Z., Liu, S., Li, S., Li, L., Zheng, L., Weng, X., Guo, X., Lu, Y., Men, W., Gao, J., & You, X. (2022). Dissociating value-based neurocomputation from subsequent selection-related activations in human decision-making. *Cerebral Cortex*, *32*(19), 4141–4155. https://doi.org/10.1093/cercor/bhab471

Loomis, A. L., Harvey, E. N., & Hobart, G. A. (1938). Distribution of disturbance-patterns in the human electroencephalogram, with special reference to sleep. *Journal of Neurophysiology*, *1*(5), 413–430. https://doi.org/10.1152/jn.1938.1.5.413

Lopes Da Silva, F. (1991). Neural mechanisms underlying brain waves: From neural membranes to networks. *Electroencephalography and Clinical Neurophysiology*, *79*(2), 81–93. https://doi.org/10.1016/0013-4694(91)90044-5

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, *4*(11), 432–440. https://doi.org/10.1016/S1364-6613(00)01545-X

Mahjoory, K., Schoffelen, J.-M., Keitel, A., & Gross, J. (2020). The frequency gradient of human resting-state brain oscillations follows cortical hierarchies. *eLife*, *9*, e53715. https://doi.org/10.7554/eLife.53715

Makeig, S., Bell, A. J., Jung, T.-P., & Sejnowski, T. J. (1995). Independent Component Analysis of Electroencephalographic Data. *Proceedings of the 8th International Conference on Neural Information Processing Systems*, 145–151.

Markello, R. D., Hansen, J. Y., Liu, Z.-Q., Bazinet, V., Shafiei, G., Suárez, L. E., Blostein, N., Seidlitz, J., Baillet, S., Satterthwaite, T. D., Chakravarty, M. M., Raznahan, A., & Misic, B. (2022). neuromaps: Structural and functional interpretation of brain maps. *Nature Methods*, *19*(11), Article 11. https://doi.org/10.1038/s41592-022-01625-w

Matsuoka, K. (1985). Sustained oscillations generated by mutually inhibiting neurons with adaptation. *Biological Cybernetics*, *52*(6), 367–376. https://doi.org/10.1007/BF00449593

Mazzoni, A., Lindén, H., Cuntz, H., Lansner, A., Panzeri, S., & Einevoll, G. T. (2015). Computing the Local Field Potential (LFP) from Integrate-and-Fire Network Models. *PLoS Computational Biology*, *11*(12), e1004584. https://doi.org/10.1371/journal.pcbi.1004584

Mendoza-Halliday, D., Major, A. J., Lee, N., Lichtenfeld, M. J., Carlson, B., Mitchell, B., Meng, P. D., Xiong, Y. (Sophy), Westerberg, J. A., Jia, X., Johnston, K. D., Selvanayagam, J., Everling, S., Maier, A., Desimone, R., Miller, E. K., & Bastos, A. M. (2024). A ubiquitous spectrolaminar motif of local field potential power across the primate cortex. *Nature Neuroscience*, 1–14. https://doi.org/10.1038/s41593-023-01554-7

Michelmann, S., Staresina, B. P., Bowman, H., & Hanslmayr, S. (2019). Speed of time-compressed forward replay flexibly changes in human episodic memory. *Nature Human Behaviour*, *3*(2), Article 2. https://doi.org/10.1038/s41562-018-0491-4

Mitzdorf, U. (1985). Current source-density method and application in cat cerebral cortex: Investigation of evoked potentials and EEG phenomena. *Physiological Reviews*, *65*(1), 37–100. https://doi.org/10.1152/physrev.1985.65.1.37

Mohan, U. R., Zhang, H., Ermentrout, B., & Jacobs, J. (2024). The direction of theta and alpha travelling waves modulates human memory processing. *Nature Human Behaviour*. https://doi.org/10.1038/s41562-024-01838-3

Molnár, M. (1994). On the origin of the P3 event-related potential component. *International Journal of Psychophysiology*, *17*(2), 129–144. https://doi.org/10.1016/0167-8760(94)90028-0

Muller, L., Chavane, F., Reynolds, J., & Sejnowski, T. J. (2018). Cortical travelling waves: Mechanisms and computational principles. *Nature Reviews Neuroscience*, *19*(5), Article 5. https://doi.org/10.1038/nrn.2018.20

Murphy, E. (2024). ROSE: A neurocomputational architecture for syntax. *Journal of Neurolinguistics*, *70*, 101180. https://doi.org/10.1016/j.jneuroling.2023.101180

Nanda, A., Johnson, G. W., Mu, Y., Ahrens, M. B., Chang, C., Englot, D. J., Breakspear, M., & Rubinov, M. (2023). Time-resolved correlation of distributed brain activity tracks E-I balance and accounts for diverse scale-free phenomena. *Cell Reports*, *42*(4), 112254. https://doi.org/10.1016/j.celrep.2023.112254

Nestvogel, D. B., & McCormick, D. A. (2022). Visual thalamocortical mechanisms of waking state-dependent activity and alpha oscillations. *Neuron*, *110*(1), 120-138.e4. https://doi.org/10.1016/j.neuron.2021.10.005

Obrig, H., Neufang, M., Wenzel, R., Kohl, M., Steinbrink, J., Einhäupl, K., & Villringer, A. (2000). Spontaneous Low Frequency Oscillations of Cerebral Hemodynamics and Metabolism in Human Adults. *NeuroImage*, *12*(6), 623–639. https://doi.org/10.1006/nimg.2000.0657

Okun, M., Naim, A., & Lampl, I. (2010). The subthreshold relation between cortical local field potential and neuronal firing unveiled by intracellular recordings in awake rats. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *30*(12), 4440–4448. https://doi.org/10.1523/JNEUROSCI.5062-09.2010

Ozen, S., Sirota, A., Belluscio, M. A., Anastassiou, C. A., Stark, E., Koch, C., & Buzsáki, G. (2010). Transcranial Electric Stimulation Entrains Cortical Neuronal Populations in Rats. *The Journal of Neuroscience*, *30*(34), 11476–11485. https://doi.org/10.1523/JNEUROSCI.5252-09.2010

Pals, M., Macke, J. H., & Barak, O. (2024). Trained recurrent neural networks develop phase-locked limit cycles in a working memory task. *PLOS Computational Biology*, *20*(2), e1011852. https://doi.org/10.1371/journal.pcbi.1011852

Parra, L. C., Spence, C. D., Gerson, A. D., & Sajda, P. (2005). Recipes for the linear analysis of EEG. *NeuroImage*, *28*(2), 326–341. https://doi.org/10.1016/j.neuroimage.2005.05.032

Payeur, A., Guerguiev, J., Zenke, F., Richards, B. A., & Naud, R. (2021). Burst-dependent synaptic plasticity can coordinate learning in hierarchical circuits. *Nature Neuroscience*, *24*(7), Article 7. https://doi.org/10.1038/s41593-021-00857-x

Pearl, J. (2009). *Causality*. Cambridge university press.

Pesaran, B., Vinck, M., Einevoll, G. T., Sirota, A., Fries, P., Siegel, M., Truccolo, W., Schroeder, C. E., & Srinivasan, R. (2018). Investigating large-scale brain dynamics using field potential recordings: Analysis and interpretation. *Nature Neuroscience*, *21*(7), Article 7. https://doi.org/10.1038/s41593-018-0171-8

Pessoa, L. (2023). The Entangled Brain. *Journal of Cognitive Neuroscience*, *35*(3), 349–360. https://doi.org/10.1162/jocn_a_01908

Picton, T. W. (1992). The P300 Wave of the Human Event-Related Potential: *Journal of Clinical Neurophysiology*, *9*(4), 456–479. https://doi.org/10.1097/00004691-199210000-00002

Pignatelli, M., Beyeler, A., & Leinekugel, X. (2012). Neural circuits underlying the generation of theta oscillations. *Journal of Physiology-Paris*, *106*(3), 81–92. https://doi.org/10.1016/j.jphysparis.2011.09.007

Pikovsky, A., Rosenblum, M., & Kurths, J. (2001). *Synchronization: A Universal Concept in Nonlinear Sciences*. Cambridge University Press; Cambridge Core. https://doi.org/10.1017/CBO9780511755743

Pinotsis, D. A., Fridman, G., & Miller, E. K. (2023). Cytoelectric coupling: Electric fields sculpt neural activity and “tune” the brain’s infrastructure. *Progress in Neurobiology*, *226*, 102465. https://doi.org/10.1016/j.pneurobio.2023.102465

Pinotsis, D. A., & Miller, E. K. (2023). In vivo ephaptic coupling allows memory network formation. *Cerebral Cortex*, *33*(17), 9877–9895. https://doi.org/10.1093/cercor/bhad251

Polanía, R., Moisa, M., Opitz, A., Grueschow, M., & Ruff, C. C. (2015). The precision of value-based choices depends causally on fronto-parietal phase coupling. *Nature Communications*, *6*(1), Article 1. https://doi.org/10.1038/ncomms9090

Polanía, R., Nitsche, M. A., Korman, C., Batsikadze, G., & Paulus, W. (2012). The importance of timing in segregated theta phase-coupling for cognitive performance. *Current Biology: CB*, *22*(14), 1314–1318. https://doi.org/10.1016/j.cub.2012.05.021

Pratt, H. (2011). Sensory ERP components. *The Oxford Handbook of Event-Related Potential Components*, 89–114.

Qasim, S. E., Fried, I., & Jacobs, J. (2021). Phase precession in the human hippocampus and entorhinal cortex. *Cell*, *184*(12), 3242-3255.e10. https://doi.org/10.1016/j.cell.2021.04.017

Qiu, C., Shivacharan, R. S., Zhang, M., & Durand, D. M. (2015). Can Neural Activity Propagate by Endogenous Electrical Field? *The Journal of Neuroscience*, *35*(48), 15800–15811. https://doi.org/10.1523/JNEUROSCI.1045-15.2015

Quinn, A. J., Lopes-dos-Santos, V., Huang, N., Liang, W.-K., Juan, C.-H., Yeh, J.-R., Nobre, A. C., Dupret, D., & Woolrich, M. W. (2021). Within-cycle instantaneous frequency profiles report oscillatory waveform dynamics. *Journal of Neurophysiology*, *126*(4), 1190–1208. https://doi.org/10.1152/jn.00201.2021

Radman, T., Ramos, R. L., Brumberg, J. C., & Bikson, M. (2009). Role of cortical cell type and morphology in subthreshold and suprathreshold uniform electric field stimulation in vitro. *Brain Stimulation*, *2*(4), 215-228.e3. https://doi.org/10.1016/j.brs.2009.03.007

Radman, T., Su, Y., An, J. H., Parra, L. C., & Bikson, M. (2007). Spike Timing Amplifies the Effect of Electric Fields on Neurons: Implications for Endogenous Field Effects. *Journal of Neuroscience*, *27*(11), 3030–3036. https://doi.org/10.1523/JNEUROSCI.0095-07.2007

Ray, S., & Maunsell, J. H. R. (2011). Different Origins of Gamma Rhythm and High-Gamma Activity in Macaque Visual Cortex. *PLOS Biology*, *9*(4), e1000610. https://doi.org/10.1371/journal.pbio.1000610

Reato, D., Rahman, A., Bikson, M., & Parra, L. C. (2010). Low-intensity electrical stimulation affects network dynamics by modulating population rate and spike timing. *Journal of Neuroscience*, *30*(45), 15067–15079.

Reddy, L., Self, M. W., Zoefel, B., Poncet, M., Possel, J. K., Peters, J. C., Baayen, J. C., Idema, S., VanRullen, R., & Roelfsema, P. R. (2021). Theta-phase dependent neuronal coding during sequence learning in human single neurons. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-021-25150-0

Reifenstein, E. T., Kempter, R., Schreiber, S., Stemmler, M. B., & Herz, A. V. M. (2012). Grid cells in rat entorhinal cortex encode physical space with independent firing fields and phase precession at the single-trial level. *Proceedings of the National Academy of Sciences*, *109*(16), 6301–6306. https://doi.org/10.1073/pnas.1109599109

Reimann, M. W., Anastassiou, C. A., Perin, R., Hill, S., Markram, H., & Koch, C. (2013). A biophysically detailed model of neocortical Local Field Potentials predicts the critical role of active membrane currents. *Neuron*, *79*(2), 375–390. https://doi.org/10.1016/j.neuron.2013.05.023

Ross, L. N., & Bassett, D. S. (2024). Causation in neuroscience: Keeping mechanism meaningful. *Nature Reviews Neuroscience*, *25*(2), Article 2. https://doi.org/10.1038/s41583-023-00778-7

Ruffini, G., Salvador, R., Tadayon, E., Sanchez-Todo, R., Pascual-Leone, A., & Santarnecchi, E. (2020). Realistic modeling of mesoscopic ephaptic coupling in the human brain. *PLOS Computational Biology*, *16*(6), e1007923. https://doi.org/10.1371/journal.pcbi.1007923

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, *11*(6), 251–257. https://doi.org/10.1016/j.tics.2007.04.004

Russo, A. A., Bittner, S. R., Perkins, S. M., Seely, J. S., London, B. M., Lara, A. H., Miri, A., Marshall, N. J., Kohn, A., Jessell, T. M., Abbott, L. F., Cunningham, J. P., & Churchland, M. M. (2018). Motor Cortex Embeds Muscle-like Commands in an Untangled Population Response. *Neuron*, *97*(4), 953-966.e8. https://doi.org/10.1016/j.neuron.2018.01.004

Sandhaeger, F., & Siegel, M. (2023). Testing the generalization of neural representations. *NeuroImage*, *278*, 120258. https://doi.org/10.1016/j.neuroimage.2023.120258

Schaworonkow, N. (2023). Overcoming harmonic hurdles: Genuine beta-band rhythms vs. contributions of alpha-band waveform shape. *PsyArXiv*. https://doi.org/10.31234/osf.io/ywv8s

Schaworonkow, N., & Voytek, B. (2021). Enhancing oscillations in intracranial electrophysiological recordings with data-driven spatial filters. *PLOS Computational Biology*, *17*(8), e1009298. https://doi.org/10.1371/journal.pcbi.1009298

Schneider, M., Broggini, A. C., Dann, B., Tzanou, A., Uran, C., Sheshadri, S., Scherberger, H., & Vinck, M. (2021). A mechanism for inter-areal coherence through communication based on connectivity and oscillatory power. *Neuron*, *109*(24), 4050-4067.e12. https://doi.org/10.1016/j.neuron.2021.09.037

Schroeder, C. E., Steinschneider, M., Javitt, D. C., Tenke, C. E., Givre, S. J., Mehta, A. D., Simpson, G. V., Arezzo, J. C., & Vaughan, H. G. (1995). Localization of ERP generators and identification of underlying neural processes. *Electroencephalography and Clinical Neurophysiology. Supplement*, *44*, 55–75.

Schurger, A., Hu, P. "Ben," Pak, J., & Roskies, A. L. (2021). What Is the Readiness Potential? *Trends in Cognitive Sciences*, *25*(7), 558–570. https://doi.org/10.1016/j.tics.2021.04.001

Shewcraft, R. A., Dean, H. L., Fabiszak, M. M., Hagan, M. A., Wong, Y. T., & Pesaran, B. (2020). Excitatory/Inhibitory Responses Shape Coherent Neuronal Dynamics Driven by Optogenetic Stimulation in the Primate Brain. *Journal of Neuroscience*, *40*(10), 2056–2068. https://doi.org/10.1523/JNEUROSCI.1949-19.2020

Shin, H., Law, R., Tsutsui, S., Moore, C. I., & Jones, S. R. (2017). The rate of transient beta frequency events predicts behavior across tasks and species. *eLife*, *6*, e29086. https://doi.org/10.7554/eLife.29086

Shirhatti, V., Borthakur, A., & Ray, S. (2016). Effect of Reference Scheme on Power and Phase of the Local Field Potential. *Neural Computation*, *28*(5), 882–913. https://doi.org/10.1162/NECO_a_00827

Skaar, J.-E. W., Haug, N., Stasik, A. J., Einevoll, G. T., & Tøndel, K. (2023). Metamodelling of a two-population spiking neural network. *PLOS Computational Biology*, *19*(11), e1011625. https://doi.org/10.1371/journal.pcbi.1011625

Staresina, B. P., & Wimber, M. (2019). A Neural Chronometry of Memory Recall. *Trends in Cognitive Sciences*, *23*(12), 1071–1085. https://doi.org/10.1016/j.tics.2019.09.011

Steriade, M., & Llinás, R. R. (1988). The functional states of the thalamus and the associated neuronal interplay. *Physiological Reviews*, *68*(3), 649–742. https://doi.org/10.1152/physrev.1988.68.3.649

Stewart, M., & Fox, S. E. (1989). Two populations of rhythmically bursting neurons in rat medial septum are revealed by atropine. *Journal of Neurophysiology*, *61*(5), 982–993. https://doi.org/10.1152/jn.1989.61.5.982

Stiefel, K. M., & Ermentrout, G. B. (2016). Neurons as oscillators. *Journal of Neurophysiology*, *116*(6), 2950–2960. https://doi.org/10.1152/jn.00525.2015

Strogatz, S. H. (2019). *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering* (2nd ed.). CRC Press. https://doi.org/10.1201/9780429492563

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus Specificity of Phase-Locked and Non-Phase-Locked 40 Hz Visual Responses in Human. *The Journal of Neuroscience*, *16*(13), 4240–4249. https://doi.org/10.1523/JNEUROSCI.16-13-04240.1996

Teplov, I. Y., Zinchenko, V. P., Kosenkov, A. M., Gaidin, S. G., Nenov, M. N., & Sergeev, A. I. (2021). Involvement of NMDA and GABA(A) receptors in modulation of spontaneous activity in hippocampal culture: Interrelations between burst firing and intracellular calcium signal. *Biochemical and Biophysical Research Communications*, *553*, 99–106. https://doi.org/10.1016/j.bbrc.2021.02.149

Ter Wal, M., Linde-Domingo, J., Lifanov, J., Roux, F., Kolibius, L. D., Gollwitzer, S., Lang, J., Hamer, H., Rollings, D., Sawlani, V., Chelvarajah, R., Staresina, B., Hanslmayr, S., & Wimber, M. (2021). Theta rhythmicity governs human behavior and hippocampal signals during memory-dependent tasks. *Nature Communications*, *12*(1), 7048. https://doi.org/10.1038/s41467-021-27323-3

Thiery, T., Lajnef, T., Jerbi, K., Arguin, M., Aubin, M., & Jolicoeur, P. (2016). Decoding the Locus of Covert Visuospatial Attention from EEG Signals. *PLOS ONE*, *11*(8), e0160304. https://doi.org/10.1371/journal.pone.0160304

Thut, G., Schyns, P., & Gross, J. (2011). Entrainment of Perceptually Relevant Brain Oscillations by Non-Invasive Rhythmic Stimulation of the Human Brain. *Frontiers in Psychology*, *2*. https://www.frontiersin.org/articles/10.3389/fpsyg.2011.00170

Tingley, D., Alexander, A. S., Quinn, L. K., Chiba, A. A., & Nitz, D. (2018). Multiplexed oscillations and phase rate coding in the basal forebrain. *Science Advances*, *4*(8), eaar3230. https://doi.org/10.1126/sciadv.aar3230

Tiruvadi, V. (2023, March 25). Measurement vs Measurement. *Medium*. https://virati.medium.com/measurement-vs-measurement-346ace68be50

Tolley, N., Rodrigues, P. L. C., Gramfort, A., & Jones, S. (2023). Methods and considerations for estimating parameters in biophysically detailed neural models with simulation based inference. *bioRxiv*, 2023.04.17.537118. https://doi.org/10.1101/2023.04.17.537118

Trakoshis, S., Martínez-Cañada, P., Rocchi, F., Canella, C., You, W., Chakrabarti, B., Ruigrok, A. N., Bullmore, E. T., Suckling, J., Markicevic, M., Zerbi, V., MRC AIMS Consortium, Baron-Cohen, S., Gozzi, A., Lai, M.-C., Panzeri, S., & Lombardo, M. V. (2020). Intrinsic excitation-inhibition imbalance affects medial prefrontal cortex differently in autistic men versus women. *eLife*, *9*, e55684. https://doi.org/10.7554/eLife.55684

Tremblay, S., Doucet, G., Pieper, F., Sachs, A., & Martinez-Trujillo, J. (2015). Single-Trial Decoding of Visual Attention from Local Field Potentials in the Primate Lateral Prefrontal Cortex Is Frequency-Dependent. *Journal of Neuroscience*, *35*(24), 9038–9049. https://doi.org/10.1523/JNEUROSCI.1041-15.2015

Ujfalussy, B. B., & Orbán, G. (2022). Sampling motion trajectories during hippocampal theta sequences. *eLife*, *11*, e74058. https://doi.org/10.7554/eLife.74058

Uludağ, K., Dubowitz, D. J., Yoder, E. J., Restom, K., Liu, T. T., & Buxton, R. B. (2004). Coupling of cerebral blood flow and oxygen consumption during physiological activation and deactivation measured with fMRI. *NeuroImage*, *23*(1), 148–155. https://doi.org/10.1016/j.neuroimage.2004.05.013

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 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.

Van Wingerden, M., Vinck, M., Lankelma, J., & Pennartz, C. M. A. (2010a). Theta-Band Phase Locking of Orbitofrontal Neurons during Reward Expectancy. *The Journal of Neuroscience*, *30*(20), 7078–7087. https://doi.org/10.1523/JNEUROSCI.3860-09.2010

Van Wingerden, M., Vinck, M., Lankelma, J. V., & Pennartz, C. M. A. (2010b). Learning-Associated Gamma-Band Phase-Locking of Action–Outcome Selective Neurons in Orbitofrontal Cortex. *The Journal of Neuroscience*, *30*(30), 10025–10038. https://doi.org/10.1523/JNEUROSCI.0222-10.2010

Vanderwolf, C. H. (1969). Hippocampal electrical activity and voluntary movement in the rat. *Electroencephalography and Clinical Neurophysiology*, *26*(4), 407–418. https://doi.org/10.1016/0013-4694(69)90092-3

Vázquez-Rodríguez, B., Avena-Koenigsberger, A., Sporns, O., Griffa, A., Hagmann, P., & Larralde, H. (2017). Stochastic resonance at criticality in a network model of the human cortex. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/s41598-017-13400-5

Vieira, P. G., Krause, M. R., & Pack, C. C. (2020). tACS entrains neural activity while somatosensory input is blocked. *PLOS Biology*, *18*(10), e3000834. https://doi.org/10.1371/journal.pbio.3000834

Vieira, P. G., Krause, M. R., & Pack, C. C. (2023). *Temporal interference stimulation disrupts spike timing in the primate brain* [Preprint]. Neuroscience. https://doi.org/10.1101/2023.09.25.559340

Vinck, M., Uran, C., & Schneider, M. (2022). *Aperiodic processes explaining rhythms in behavior: A matter of false detection or definition?*

Vöröslakos, M., Takeuchi, Y., Brinyiczki, K., Zombori, T., Oliva, A., Fernández-Ruiz, A., Kozák, G., Kincses, Z. T., Iványi, B., Buzsáki, G., & Berényi, A. (2018). Direct effects of transcranial electric stimulation on brain circuits in rats and humans. *Nature Communications*, *9*(1), 483. https://doi.org/10.1038/s41467-018-02928-3

Vyas, S., Golub, M. D., Sussillo, D., & Shenoy, K. V. (2020). Computation Through Neural Population Dynamics. *Annual Review of Neuroscience*, *43*(1), 249–275. https://doi.org/10.1146/annurev-neuro-092619-094115

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

Warman, E. N., Grill, W. M., & Durand, D. (1992). Modeling the effects of electric fields on nerve fibers: Determination of excitation thresholds. *IEEE Transactions on Bio-Medical Engineering*, *39*(12), 1244–1254. https://doi.org/10.1109/10.184700

Waschke, L., Donoghue, T., Fiedler, L., Smith, S., Garrett, D. D., Voytek, B., & Obleser, J. (2021). Modality-specific tracking of attention and sensory statistics in the human electrophysiological spectral exponent. *eLife*, *10*, e70068. https://doi.org/10.7554/eLife.70068

Waschke, L., Tune, S., & Obleser, J. (2019). Local cortical desynchronization and pupil-linked arousal differentially shape brain states for optimal sensory performance. *eLife*, *8*, e51501. https://doi.org/10.7554/eLife.51501

Weaver, J. C., & Astumian, R. D. (1990). The Response of Living Cells to Very Weak Electric Fields: The Thermal Noise Limit. *Science*, *247*(4941), 459–462. https://doi.org/10.1126/science.2300806

Weaver, J. C., Vaughan, T. E., & Martin, G. T. (1999). Biological Effects Due to Weak Electric and Magnetic Fields: The Temperature Variation Threshold. *Biophysical Journal*, *76*(6), 3026–3030. https://doi.org/10.1016/S0006-3495(99)77455-2

Weiss, S. A., & Faber, D. S. (2010). Field Effects in the CNS Play Functional Roles. *Frontiers in Neural Circuits*, *4*, 15. https://doi.org/10.3389/fncir.2010.00015

Whittington, M. A., Traub, R. D., Kopell, N., Ermentrout, B., & Buhl, E. H. (2000). Inhibition-based rhythms: Experimental and mathematical observations on network dynamics. *International Journal of Psychophysiology*, *38*(3), 315–336. https://doi.org/10.1016/S0167-8760(00)00173-2

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), Article 8. https://doi.org/10.1038/nn.3764

Woodward, J. (2003). *Making Things Happen: A Theory of Causal Explanation*. Oxford University Press.

Ylinen, A., Bragin, A., Nadasdy, Z., Jando, G., Szabo, I., Sik, A., & Buzsaki, G. (1995). Sharp wave-associated high-frequency oscillation (200 Hz) in the intact hippocampus: Network and intracellular mechanisms. *The Journal of Neuroscience*, *15*(1), 30–46. https://doi.org/10.1523/JNEUROSCI.15-01-00030.1995

Zhang, M., Ladas, T. P., Qiu, C., Shivacharan, R. S., Gonzalez-Reyes, L. E., & Durand, D. M. (2014). Propagation of epileptiform activity can be independent of synaptic transmission, gap junctions, or diffusion and is consistent with electrical field transmission. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(4), 1409–1419. https://doi.org/10.1523/JNEUROSCI.3877-13.2014

Zheng, C., & Colgin, L. L. (2015). Beta and gamma rhythms go with the flow. *Neuron*, *85*(2), 236–237. https://doi.org/10.1016/j.neuron.2014.12.067

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