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Challenges and Approaches in the Study of Neural Entrainment

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Abstract

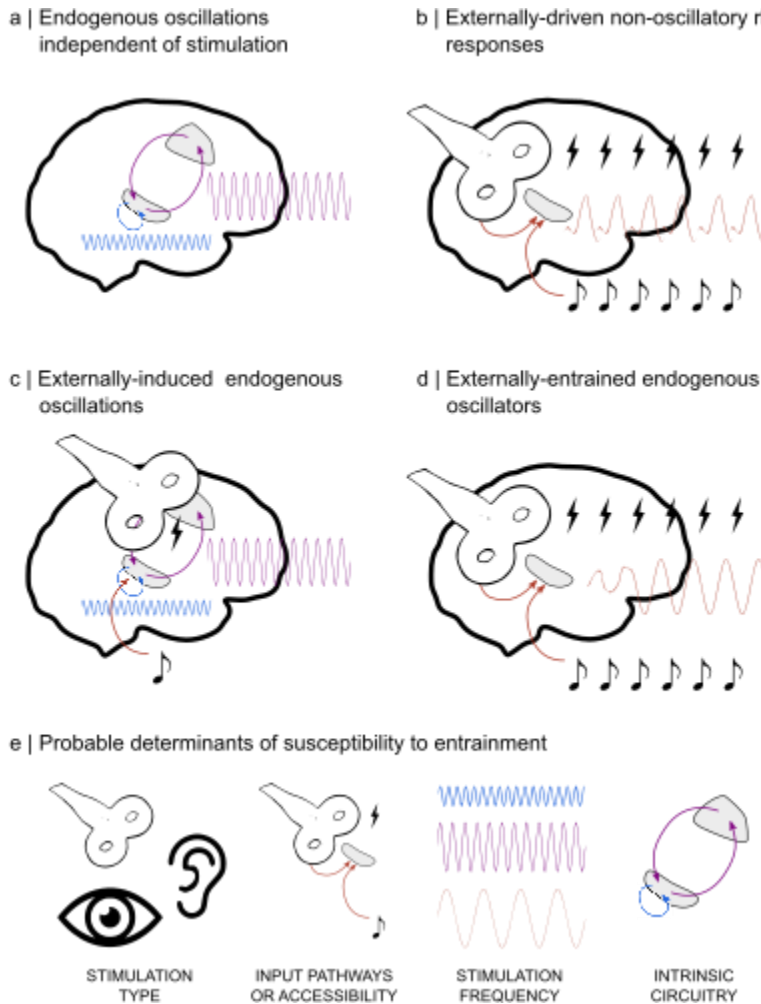
When exposed to rhythmic stimulation, the human brain displays rhythmic activity across sensory modalities and regions. Given the ubiquity of this phenomenon, how sensory rhythms are transformed into neural rhythms remains surprisingly inconclusive. An influential model posits that endogenous oscillations entrain to external rhythms, thereby encoding environmental dynamics and shaping perception. However, research on neural entrainment faces multiple challenges, from ambiguous definitions to methodological difficulties when endogenous oscillations need to be identified and disentangled from other stimulus-related mechanisms that can lead to similar phase-locked responses. Yet, recent years have seen novel approaches to overcome these challenges, including computational modelling, insights from dynamical systems theory, sophisticated stimulus designs, and study of neuropsychological impairments. This review outlines key challenges in neural entrainment research, delineates state-of-the-art approaches, and integrates findings from human and animal neurophysiology to provide a broad perspective on the usefulness, validity and constraints of oscillatory models in brain-environment interaction.

1 Rhythms in neural and sensory dynamics

2 Rhythmic activity is a prominent signature of intra- and extracranial brain recordings (Buzsáki et
3 al., 2013; Jones, 2016). Such patterns, commonly referred to as neural oscillations, have been
4 observed in various species including insects (Popov and Szyszka, 2020; Greenfield and Merker,
5 2023), rodents (Jacobs, 2014), humans and non-human primates (Buzsáki and Vöröslakos,
6 2023). Neural oscillations are an endogenous property of neural circuits, that is, they can exist in
7 the absence of any sensory stimulation (Figure 1a), and even in vitro, when the tissue is isolated
8 from dynamic input (Florez et al., 2015; de la Prida et al., 2019). They are thought to reflect
9 coordinated activity of neural ensembles within networks of brain areas, in support of various
10 cognitive functions (Bressler and Kelso, 2001; Buzsáki and Draguhn, 2004; Uhlhaas et al., 2010).
11 For instance, alpha oscillations (~8-14 Hz) in sensory cortices are assumed to reflect “pulses” of
12 inhibition that support attentional processes (Klimesch et al., 2007; Jensen and Mazaheri, 2010;
13 Jensen, 2024), while beta oscillations (~15-30 Hz) in motor-related areas have been linked to
14 movement preparation (Barone and Rossiter, 2021) as well as sensory predictive processes
15 (Arnal, 2012; Fujioka et al., 2012). Theta oscillations (~4-7 Hz) are prevalent in a number of
16 regions, dominating hippocampal activity to support spatial navigation and episodic memories
17 (Herweg et al., 2020; Rudoler et al., 2023) while playing an important role for speech processing
18 in the auditory cortex (Doelling et al., 2014; Zoefel and Kösem, 2024). Gamma oscillations have
19 been ascribed a critical role in sensory processing (Gray, 1999; Buzsáki and Wang, 2012; Vinck
20 et al., 2023), inter-areal communication (Fries, 2015), and memory (Howard et al., 2003; Griffiths
21 and Jensen, 2023). The importance of these rhythms for healthy brain function is supported by a
22 multitude of studies demonstrating disrupted dynamics in brain disorders associated with
23 cognitive deficits, such as Alzheimer’s, schizophrenia, autism, and dyslexia (Uhlhaas and Singer,
24 2006; Başar, 2013; Rojas and Wilson, 2014; Leicht et al., 2016; van Niffterick et al., 2023).

25 A key scenario in which rhythmic neural activity is observed is during periodic sensory stimulation,
26 in a frequency range that matches the stimulation frequency (and its integer multiples, called
27 harmonics), which is well-documented in invasive and non-invasive electrophysiological
28 recordings (Adrian and Matthews, 1934; Walter and Walter, 1949; Kimura, 1980). This presence
29 of rhythmic activity can substantiate as periodic responses, increased spectral amplitude, or as a
30 consistent relationship between neural and stimulation phase. A prominent hypothesis is that
31 these rhythmic brain responses reflect coupling of endogenous neural oscillations to the rhythmic
32 external drive (Lakatos et al., 2008). This notion relies on the assumption that spontaneous
33 neuronal oscillations are self-sustained oscillators as defined in dynamical systems theory, with
34 corresponding properties such as entrainment and resonance (Pikovsky et al., 2001; Helfrich et
35 al., 2019; Strogatz, 2019; van Bree et al., 2022). Mechanistically, it has been proposed that the
36 high-excitability phase of neural oscillations becomes aligned to relevant events in a rhythmic
37 sequence, thereby boosting their processing (Lakatos et al., 2008; Schroeder and Lakatos, 2009).
38 This theory has become highly influential and applied to many scientific questions that entail
39 dynamic interaction with the environment. For example, in current models of speech perception
40 (Giraud and Poeppel, 2012; Meyer et al., 2020; Poeppel and Assaneo, 2020; Kazanina and
41 Tavano, 2023; Zoefel and Kösem, 2024), the similarity between frequencies of neural oscillations
42 and the various “building blocks” in human speech (e.g., prosody, words, syllables, and

43 phonemes) has inspired the idea that oscillations parse sensory information or shape its
 44 representation by synchronizing to external rhythms (Henry and Obleser, 2012; Gnanateja et al.,
 45 2022). In general, the oscillatory entrainment hypothesis provides an elegant and efficient
 46 explanation of how brain dynamics can interact with those in the environment.



47

48 **Figure 1.** A neural oscillation is only one of a variety of related phenomena that contribute to phase-locked
 49 stimulus responses, and that are difficult to dissociate experimentally. **a)** Endogenous neural oscillations
 50 are generated within local brain regions in the course of cognitive processes (generally thought to be higher-
 51 frequency oscillations, e.g. gamma), or between regions (lower frequency oscillations). **b)** Introducing
 52 perceptual information through sensory pathways which contains periodicity, such as music and language,
 53 or stimulating the brain directly via electrical or magnetic techniques such as transcranial magnetic
 54 stimulation, can generate rhythmic brain responses; however, the existence of rhythmic neural activity need
 55 not imply involvement of a neural oscillator if activity can be accounted for by a series of evoked responses.
 56 **c)** Sensory or other stimulation might be used to induce neural oscillations (as when a signal magnetic
 57 pulse causes a circuit to reverberate at its preferred frequency) without implying entrainment. **d)** A series
 58 of periodic inputs may gradually synchronize and entrain a neural circuit that has resonant properties.
 59 Practically, it can be difficult to distinguish between **b)** and **d)** in neural data. Factors that might influence
 60 brain regions' and circuits' susceptibility to neural entrainment by external stimuli are illustrated in **e)**.

61 The term “entrainment” originates from dynamical systems theory and assumes the involvement
 62 of an oscillator coupled to a periodic input either uni- or bi-directionally, a definition we adopt here

63 unless stated otherwise (for more details, see Section 2.1). However, this term has been
64 expanded and is now used liberally in cognitive neuroscience to describe any case of phase-
65 locked neural responses (Lakatos et al., 2019; Obleser and Kayser, 2019). Although more neutral
66 terms like “tracking” have been suggested (cf. Banki et al., 2022), “entrainment” continues to be
67 a popular label for stimulus-aligned brain responses without strong evidence for an oscillatory
68 origin. For some scientific applications of rhythmic sensory stimulation, knowledge of this origin
69 may indeed not be required. One example is the concept of “frequency tagging”, where the
70 rhythmic brain response is used as a readout of the participant’s attentional state but the term
71 “entrainment” is less frequently used (Regan, 1966; Müller et al., 1998; Zhigalov et al., 2019;
72 Drijvers et al., 2021). Applications for rhythmic brain responses can also be found in clinical
73 research, e.g. in the identification of biomarkers (Sivarao, 2015; Javitt et al., 2020) and as a
74 therapeutic tool in the treatment of Alzheimer’s disease (Iaccarino et al., 2016). Yet in many cases
75 it is essential to determine the involvement of entrained oscillations, as the computational
76 principles that feature in models, such as phase-based encoding or prediction, rely on properties
77 of oscillators such as period correction and resonance.

78 The mechanistic origins of neural entrainment, and in particular the role of neural oscillations, has
79 proven to be controversial, with diverging results and positions in the literature (Keitel et al., 2014,
80 2022; Haegens and Zion Golumbic, 2018; Zoefel et al., 2018; Meyer et al., 2020; Doelling and
81 Assaneo, 2021; van Bree et al., 2022). For example, identification of endogenous neural
82 oscillations – i.e. an involvement of a neural circuit that can produce rhythmic activity on its own
83 (Figure 1a) – during rhythmic stimulation is not always straightforward. Thus, the model of neural
84 oscillations entrained to sensory rhythms faces multiple challenges that can seem to question the
85 usefulness of such a model. Considering the prevalence of rhythmic stimulation in cognitive
86 neuroscience, and the diverging evidence in its effect on neural mechanisms, this review aims to
87 outline significant challenges in the research on neural entrainment in sensory systems, as well
88 as novel approaches to overcome methodological concerns and miscommunication. We highlight
89 studies that have employed these approaches to provide evidence for an involvement of
90 endogenous oscillations in the processing of rhythmic input as well as the constraints on such
91 mechanisms, and critically discuss the usefulness of an “oscillator” to study neural dynamics.

92 2. Challenges in the study of neural entrainment

93 2.1 Definitions of terms are variable

94
95 A key issue in the field of neural entrainment is variability in its definitions. While the terms
96 “synchronization”, “oscillation”, and “entrainment” have mathematical definitions in dynamical
97 systems theory (Pikovsky et al., 2001), they are more ambiguous in cognitive neuroscience.
98 According to dynamical systems theory, “entrainment” involves an active (uni- or bidirectional)
99 influence between oscillators whereas “synchronization” implies a zero-lag phase relationship
100 between two processes but does not necessarily involve oscillators (Bittman, 2021). The definition
101 of these terms is often altered in cognitive neuroscience so that “entrainment” simply refers to

102 neural responses phase-locked to sensory events (cf. the “broad sense” in Obleser and Kayser,
103 2019). Likewise, “synchronization” includes other phase lags besides zero, to consider potential
104 delays between the occurrence of an event and its neural processing. Finally, rhythmic signals
105 are often termed “oscillations” regardless of the source of rhythmicity, a challenge we describe in
106 Section 2.3 and illustrate in Figure 1. The importance of embracing the mathematical definition of
107 these terms in cognitive neuroscience has been discussed elsewhere (Helfrich et al., 2019;
108 Lakatos et al., 2019; Obleser and Kayser, 2019). Rather than reiterating the relevance of these
109 “true” definitions, we here propose that authors’ hypotheses on the underlying mechanisms
110 should be detailed as precisely as possible in studies of phase-locked signals. Outlining these
111 assumptions could be guided by questions like: Does the study assume that endogenous
112 oscillatory dynamics underlie the observed response to stimulation? Can this oscillatory rhythm
113 be observed in absence of the stimulus, i.e., does it emerge from a neural circuit that produces
114 spontaneous oscillations within the investigated frequency band? What are the neural
115 mechanisms through which the external stimulus may or may not be able to modulate activity in
116 the circuit? As we will argue in this review, providing answers to these questions will make future
117 studies more consistent, replicable, and easier to interpret.

118 2.2 Properties of neural generators are rarely considered

119 A large portion of the literature on neural entrainment is based on electroencephalography (EEG)
120 and magnetoencephalography (MEG) data from human participants, or on extracellular fields
121 measured in rodents and primates. These methods do not provide access to the low-level circuitry
122 underlying the recorded rhythms, leading to ambiguity in how experimenters define entrainment
123 at the neuronal level. Does rhythmic stimulation need to modulate the postsynaptic potential or
124 spiking of individual neurons in the circuit, or should it influence the complex dynamical processes
125 generating the oscillation? One example is the 40-Hz gamma rhythm, which has become a
126 popular target for entrainment by visual stimulation (Iaccarino et al., 2016). This work is opposed
127 by studies arguing that spontaneously generated, native gamma oscillations do not entrain to a
128 visual flicker (Duecker et al., 2021; Schneider et al., 2023; Soula et al., 2023). To solve the
129 divergence in the literature, should we consider the endogenous oscillator to be entrained only if
130 the stimulation affects the circuit of pyramidal neurons and interneurons responsible for
131 generating gamma rhythms spontaneously? Clearly stating the criteria for evidence of
132 entrainment in each study may help reconcile the conflicting findings in the literature.

133
134 Furthermore, entrainment implies that properties of the neural circuit govern which stimulus
135 features and rates drive its activity, amplifying only certain stimuli for downstream processing.
136 Neurons and their ensembles are selective to features, complexity, frequency and timing of
137 sensory input and therefore do not respond equally to each type of incoming information (Figure
138 1e). For a neuronal circuit to be entrained by rhythmic sensory stimulation, the synaptic input
139 should be sensitive to the input and faithfully maintain its timing. However, non-linear
140 transformations of the sensory input during low-level processing modifies the signal as it
141 propagates to higher-order cortical regions (Gautam et al., 2024; Schneider et al., 2023),
142 potentially preventing or altering entrainment in areas beyond the sensory systems.

143

144 In addition, some oscillations may have functional properties to which an adaptation to sensory
145 input would be counterproductive, such as when they provide a temporal structure to neural
146 processing (Lisman and Jensen, 2013; ten Oever et al., 2024). In this case, the oscillation might,
147 at the risk of losing internal stability, not adapt immediately to the timing of sensory input. In
148 practice however, such an “unentrainability” is difficult to demonstrate, as it might simply result
149 from the mismatch between entraining stimulus and the “preference” of the oscillator, described
150 in the preceding paragraph. Nevertheless, the presence of oscillatory dynamics in a cortical region
151 at rest does not allow any inference about whether the corresponding neural generator can be
152 entrained by a stimulus. At the same time, a lack of evidence for entrainment does not suffice to
153 refute the presence of a neural oscillator which may oscillate but not entrain. Both the presence
154 and entrainability of an oscillator must be established independently.

155

156 2.3 Both endogenous rhythms and other stimulus-related signals 157 may contribute to stimulus-locked brain activity

158

159 It is a recurring question whether rhythmic brain activity during rhythmic stimulation reflects an
160 entrainment of neural oscillations to the stimulus (Figure 1d), over and above the responses that
161 are inherently evoked by each individual event in the rhythmic sequence and together form a
162 regular pattern that reflects the rhythmicity of the stimulus (Figure 1b; Walter and Walter, 1949;
163 Keitel et al., 2014; Zoefel et al., 2018). This question is not just one of semantics as the underlying
164 mechanisms will have distinct effects on downstream processing and cognitive functions (Breska
165 and Deouell, 2017a; Doelling and Assaneo, 2021). Considering that sensory systems respond to
166 a wide range of stimulation frequencies (Herrmann, 2001; Brugge et al., 2009; Duecker et al.,
167 2021), but also selectively amplify sensory rhythms at certain frequencies (Picton et al., 1987;
168 Herrmann, 2001), it is likely that both endogenous oscillatory dynamics and stimulus-evoked
169 responses contribute to brain responses during rhythmic stimulation, and it is therefore
170 challenging to separate them in a given recording. Notably, this issue is not restricted to the
171 interpretation of the neurophysiological data. If rhythmic behavioral responses (e.g., detection of
172 a target) are measured during a rhythmic stimulus, it cannot be ruled out that these are due to
173 masking effects at regular moments in time (e.g., a target might be easier to detect during gaps
174 in a rhythmic sequence). Furthermore, if rhythmic behavioral responses are observed during
175 transcranial alternating current stimulation (tACS), often assumed to entrain neural oscillations
176 (Herrmann et al., 2013), then the behavioral rhythm might simply reflect the alternating current
177 applied (most current injected at the peak and trough of the tACS signal) rather than an
178 endogenous neural oscillation (Zoefel, 2018; van Bree et al., 2021).

179

180 Periodicities in neural activity and behavior can also be explained by processes linked to temporal
181 anticipation in the periodic occurrence of events, such as interval-based prediction. The brain is
182 capable of learning an association between a cue and a specific interval initiated by it, as is
183 classically demonstrated in eyeblink conditioning (Christian and Thompson, 2003). It was also
184 shown that this ability goes beyond motor timing, as predictions from cue-interval associations
185 can also proactively guide attentional preparation (Coull and Nobre, 1998). This effect is

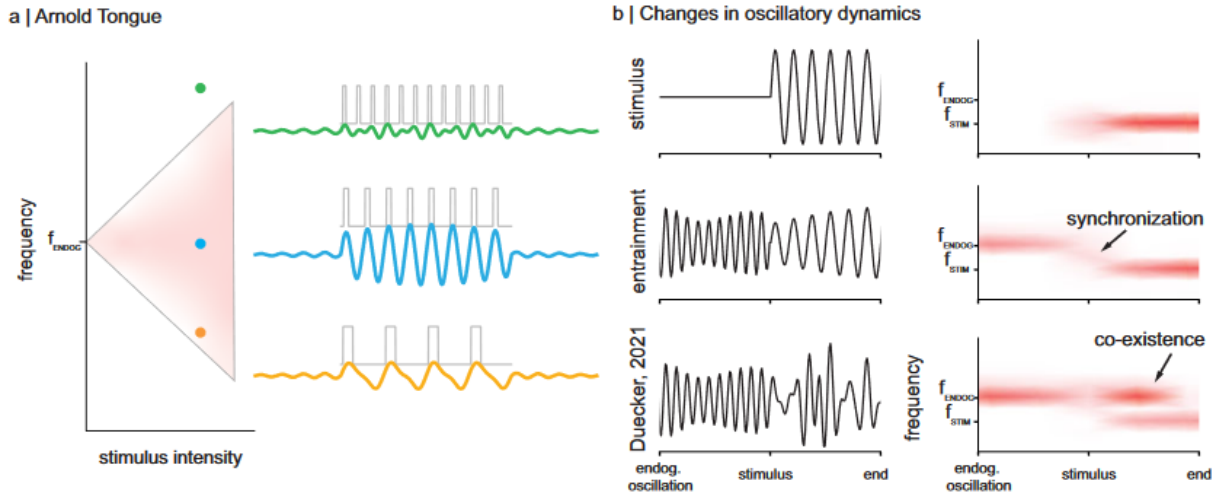
186 accompanied by adjustment of ramping activity, and anticipatory modulations of band-limited
187 activity, e.g. in alpha and beta bands (Miniussi et al., 1999; Rohenkohl and Nobre, 2011).
188 Critically, recent work that directly compared the behavioral and neural expressions of aperiodic
189 interval-based prediction with those of rhythmic streams, found that they were overlapping during
190 stream presentation. This included both phase alignment of low-frequency oscillations that match
191 the rhythm/interval frequency, as well as amplitude modulations at various frequencies (Breska
192 and Deouell, 2017b). Therefore, as a periodic stream is inherently composed of a set of
193 concatenated intervals, it is difficult to rule out that periodic alignment and fluctuations do not
194 reflect repeated operation of such non-oscillatory, discrete interval prediction mechanisms.

195 3. Approaches to identify neural entrainment

196 Addressing these challenges, we highlight here recent attempts to identify neural mechanisms
197 underlying phase-locked neural responses to rhythmic stimulation. Given their prominence in the
198 field, we focus on experimental settings that are designed to identify endogenous oscillations. Our
199 aim is to emphasize that the phenomenon of neural phase-locking to a rhythmic stimulus should
200 be studied and considered on a case-by-case basis to identify the underlying principles under
201 which the neural response to rhythmic stimulation can be categorized as neural entrainment.
202 We organize this section into approaches attacking distinct components of oscillatory behavior as
203 defined by dynamical systems theory. These approaches have often led to competing answers
204 even within the same domain, in which case we discuss possible explanations. Finally, we
205 conclude by synthesizing these findings across domains to characterize the diversity of underlying
206 mechanisms within the capabilities of neural function and how these transformations help to
207 construct the neurocognitive experience.

208 3.1 Changes in pre-existing oscillatory dynamics by an external 209 drive

210 One approach to identify endogenous oscillations in entrained brain responses in EEG and MEG
211 recordings is to focus on changes in oscillatory dynamics that were present prior to the rhythmic
212 external drive. For stimulation in the alpha band, this approach has been applied to the effect of
213 visual flicker (Notbohm et al., 2016). Prior to the flicker, the authors identified the individual alpha
214 frequency for each participant based on the resting-state EEG. They then tested how this
215 frequency relates to the flicker frequencies and intensities that led to the strongest phase-locking
216 between the EEG signal and the stimulus. Indeed, the authors demonstrated strongest phase-
217 locking if the visual flicker was centered at the individual alpha frequency, and furthermore that
218 higher amplitudes of flicker were required to synchronize alpha at wider ranges of frequencies.
219 This represents a known property of physical oscillators (Pikovsky et al., 2001) commonly referred
220 to as Arnold Tongues, which clearly demonstrate the eigenfrequency of the oscillator and how its
221 internal dynamics govern its response to stimulus rates at or near this “preferred” frequency
222 (Figure 2a).
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Figure 2. a) Resonance zones known as Arnold tongues govern oscillatory dynamics. Oscillators have preferred frequencies (f_{endog}), wherein the frequency range over which oscillations may be induced is a function of the amplitude of the stimulus. Oscillators are more difficult to entrain at non-preferred frequencies. **b)** Investigating changes in oscillatory dynamics by sensory stimulation (left: surrogate time series, right: spectrogram). Top panel: Properties of oscillatory dynamics (e.g., peak frequency) are identified in the interval before the rhythmic stimulus. Middle panel: If an endogenous oscillator is successfully entrained by a stimulus, it changes its frequency accordingly (within its preferred range). Bottom panel: A comic illustration of results from Duecker et al., 2021. Endogenous gamma oscillations were not entrained and co-existed with flicker responses in the MEG signal.

236 Many studies have demonstrated preferred stimulus rates. The auditory system, for example,
237 seems to have several preferred stimulus rates: one closer to the typical syllable rate of speech
238 (~4-8 Hz; Poeppel and Assaneo, 2020; L'Hermite and Zoefel, 2023; Zoefel and Kösem, 2024),
239 the other around 40 Hz, at which frequency a response known as the auditory steady state
240 response (ASSR) can be robustly driven (Galambos et al., 1981; Picton et al., 1987; Ross et al.,
241 2003). In contrast to the visual domain, alpha and beta bands do not phase-lock well to auditory
242 stimuli at matching rates (Teng et al., 2017; Weisz and Lithari, 2017; Teng and Poeppel, 2020).
243 Additional preferred frequencies appear to exist in higher frequency bands centred on 80 and 200
244 Hz, which may relate to processing vocal pitch (Tichko and Skoe, 2017; Coffey et al., 2021).
245 Although the presence of such preferred rates speaks for an involvement of a neural oscillator,
246 there are scenarios in which evoked responses can have similar preferences. For instance, if
247 responses evoked by individual events in a regular stimulus overlap, their summed response will
248 be higher than if they do not overlap, leading to a preferred rate even without underlying oscillatory
249 mechanism (Edwards and Chang, 2013). A demonstration of Arnold Tongues, i.e. a restricted
250 range of phase-locking which widens with increased stimulus amplitude (Figure 2a), is therefore
251 crucial for the identification of neural entrainment.

252

253 Following a similar logic, Duecker et al. (2021) combined MEG with a rapid visual flicker (>50 Hz)
254 to investigate entrainment and resonance in the gamma-band (Figure 2b). This stimulation
255 technique has gained increasing popularity as Rapid Invisible Frequency Tagging (RIFT) to probe
256 cortical excitability with high temporal resolution while reducing the visibility of the flicker (Zhigalov
257 et al., 2019; Pan et al., 2021; Minarik et al., 2023). When applied to an invisible patch in the

258 background colour, i.e. in absence of identifiable gamma oscillations prior to the stimulation, the
259 rapid flicker evoked identifiable responses to stimulation frequencies of up to 80 Hz. However,
260 the visual cortex did not seem to selectively amplify frequencies in the stimulation range (Duecker
261 et al., 2021). To investigate whether the visual flicker can entrain endogenous oscillations,
262 Duecker and colleagues first induced gamma oscillations using a moving grating stimulus
263 (Hoogenboom et al., 2006, also van Pelt et al., 2012). The rapid flicker was then imposed on the
264 grating, which allowed the authors to investigate changes in ongoing oscillations. Importantly,
265 there was no evidence that the phase or frequency of the grating-induced gamma rhythm
266 synchronized to the flicker, but instead, the two activities seemed to co-exist in early visual cortex
267 (Figure 2b, bottom). Indeed, MEG beamforming localized the flicker response to primary visual
268 cortex, while the gamma oscillations were strongest in secondary visual cortex. Moreover, the
269 frequency inducing the strongest flicker response was robustly lower than the peak frequency of
270 the gamma oscillations. These findings have been supported by a study investigating temporal
271 response functions in the gamma band in response to a broadband flicker applied to moving
272 gratings (Zhigalov et al., 2021). The authors found that the peak frequency of the perceptual
273 “gamma echo” was significantly lower than the frequency of the endogenous gamma oscillations.

274
275 Duecker et al. (2021) hypothesized that entrainment may have been prevented by the low-pass
276 filter properties of the visual system (Hawken et al., 1996; Connelly et al., 2016). Moreover, the
277 flicker may have been unable to modulate the activity of the inhibitory interneurons that are known
278 to be critically involved in generating gamma oscillations (Traub et al., 1996). Indeed, these
279 hypotheses have since been supported by intracranial recordings in mice, showing that a visual
280 flicker at 40 Hz is attenuated across the ventral stream (Schneider et al., 2023). This finding was
281 further attributed to the low-pass filter properties of cortical pyramidal neurons (Schneider et al.,
282 2023; also see Soula, 2023). Moreover, while gamma oscillations have long been hypothesized
283 to coordinate communication in the visual system (Fries, 2015), recent work suggests that
284 instead, gamma oscillations carry information about the predictability of the visual input (Peter et
285 al., 2019; Vinck et al., 2023). As such, the mechanisms underlying gamma oscillations in visual
286 cortex may have prevented entrainment by external stimuli.

287 3.2 Entrainment echoes after stimulus offset

288 Another approach to leverage the oscillator’s predicted temporal dynamics is to focus on
289 “entrainment echoes” - rhythmic brain responses that are produced by a rhythmic stimulus but
290 outlast it briefly, reflecting reverberation of the oscillating circuit (Hanslmayr et al., 2014; van Bree
291 et al., 2021). As these echoes are measured after (rather than during) a rhythmic stimulus,
292 alternative explanations (such as regular evoked responses, cf. Section 2.3, Figure 1b) are more
293 straightforward to rule out. A methodological caveat for the identification of entrainment echoes
294 is the “temporal smearing” induced by spectral analysis methods (de Cheveigné and Nelken,
295 2019) required to estimate frequency, amplitude or phase of the signal (e.g., filtering, wavelet
296 analysis, FFT), and which can produce spurious entrainment echoes by artificially “prolonging”
297 stimulus-related activity beyond stimulus offset. Nevertheless, multiple studies have
298 demonstrated such echoes even when this issue was controlled for (see also Hanslmayr et al.,
299 2014; Spaak et al., 2014; Hickok et al., 2015; Lerousseau et al., 2021).

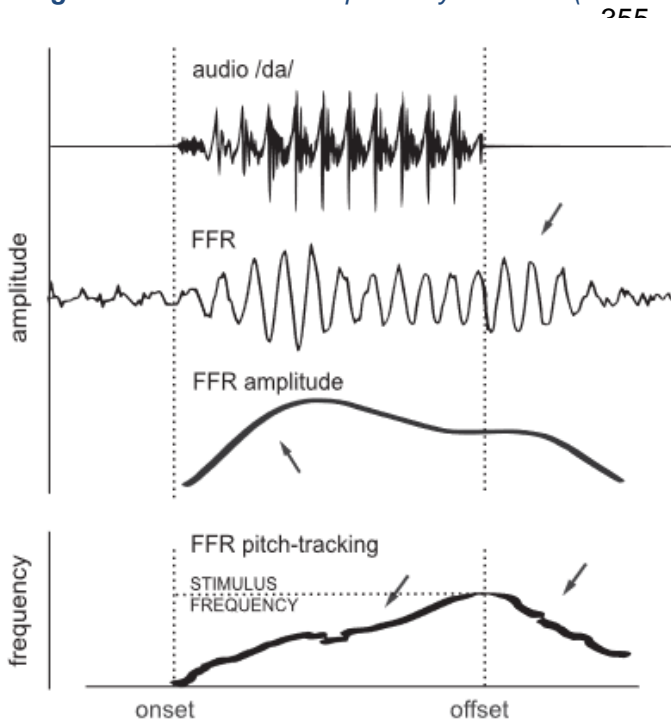
300
301 Van Bree et al (2021) tested for entrainment echoes in magnetoencephalography (MEG) after
302 intelligible or unintelligible noise-vocoded speech, presented rhythmically at 2 Hz or 3 Hz. They
303 found that rhythmic MEG responses, specific to the stimulation rate, outlasted the rhythmic
304 speech, but only when it was intelligible. These echoes seemed to originate from the cerebellum
305 and trigger connectivity with left inferior frontal regions (Zoefel et al., 2024). As described in this
306 review, speech is not the only acoustic stimulus that can produce evidence for entrainment. The
307 speech-specificity of the effect should therefore not be interpreted as a demonstration that only
308 speech can entrain oscillations in audition. However, it implies that neurons involved in oscillatory
309 circuits may be more or less sensitive to specific stimulus features, and illustrates that not all
310 stimuli produce the same after effects (cf. Section 2.2). Another line of studies used rhythmic tone
311 or noise sequences to test for entrainment echoes in auditory perception. Rhythmic changes in
312 the detection of a short pure tone were only observed after the offset of rhythmic sequences when
313 they were presented between 2 and 8 Hz (Farahbod et al., 2020; L’Hermite and Zoefel, 2023), a
314 frequency range critical for human communication and music perception. This finding
315 demonstrates, in addition to a presence of entrainment echoes, preferred rates for auditory
316 perception (cf. Section 3.1). Finally, tACS at 3 Hz leads to rhythmic changes in the accuracy of
317 word report at the corresponding rate that outlast the electric stimulation (van Bree et al 2021).
318 This finding represents evidence that tACS can also entrain endogenous oscillations as often
319 assumed (Herrmann et al., 2013).

320 It is important to note that not all studies have identified signatures of entrainment echoes in the
321 low-frequency range. Oscillatory reverberation should facilitate detection of near-threshold targets
322 appearing at on-beat times when compared to detection of off-beat targets or those presented
323 after aperiodic stimulation. However, no such patterns were found in some cases (Lin et al., 2022;
324 Sun et al., 2022; cf. Keitel et al., 2022). L’Hermite and Zoefel (2023) showed that entrainment
325 echoes in audition might be organized tonotopically. Accordingly, moments of most accurate
326 target detection after a rhythmic (~6-8 Hz) tone stimulus depended on the difference in sound
327 frequency between entrainer and target. Moreover, for identical sound frequencies, target
328 detection was most accurate at off-beat times when stimulation rate was constant across trials,
329 but on-beat when the rate was variable, an effect interpreted as repetition-related habituation only
330 during constant stimulation. Thus, how entrainment echoes manifest in perception might be more
331 complex than thought and depend on stimulus properties as well as their larger context. This
332 conclusion might explain some of the null effects described.

333 Another recent study combined this approach with computational modelling and MEG, to study
334 the role of oscillatory mechanisms in speech perception (Oganian et al., 2023). The focus was on
335 perception of naturalistic speech, which has typical non-isochronous temporal dynamics, rather
336 than rhythmized speech as in e.g., poetry. The authors asked whether the well-known
337 observation of phase alignment between human scalp recording and the speech envelope (Luo
338 and Poeppel, 2007) reflects oscillatory entrainment, or alternatively, encoding by evoked
339 responses. Generative computational models of these two mechanisms provided time-resolved
340 predictions of the spectral and temporal dynamics of phase alignment during stimulus-free pauses
341 in the speech signal. Critically, only the oscillator model predicted stable phase alignment during
342 pauses, resulting from oscillatory reverberation. These predictions were then compared to MEG

343 data recorded while participants were listening to the same speech stimulus as used in model
 344 simulations. The results indicated that both the spectral distribution and the temporal dynamics of
 345 phase alignment were in line with the evoked response model, with no sustained phase alignment
 346 due to oscillatory reverberation. These findings stand against the idea that oscillatory entrainment
 347 is involved in speech perception in natural settings, where speech mostly deviates from isochrony.
 348 On the other hand, some of the above-described entrainment echoes were specific to intelligible
 349 speech (van Bree et al., 2021; Zoefel et al., 2024), which instead would suggest that an
 350 entrainment mechanism tailored to process human speech does exist. Although other reasons
 351 for this discrepancy still need to be identified, it again highlights the strong context dependence
 352 of oscillatory mechanisms (Figure 1e), and their interaction with both stimulus properties and other
 353 non-oscillatory processes.

354 **Figure 3.** *The FFR to the speech syllable /da/ (first row) shows several cycles of oscillations after stimulus*



offset, i.e. an entrainment echo (second row). Computing the amplitude over successive small time windows shows that peak amplitude is reached only after 4-5 cycles (third row), and that the frequency converges from a hypothetical preferred frequency to the stimulus frequency over time, and relaxes back towards the preferred frequency after stimulus offset (fourth row). Modified from Coffey et al., 2021.

Phase-locked responses to higher stimulus rates (~80 - 500 Hz) observed during stimulus presentation are often termed the frequency following response (FFR; Figure 3). FFRs are closely tied to periodicity present in the environment, which is critical for perceiving vocal communication and music (Krizman & Kraus 2019; Coffey et al. 2019). The transfer of pitch information is observable non-invasively using EEG/MEG as high-frequency neural evoked responses (Coffey et al., 2016). Recently, several works

376 have reported that the FFR extends beyond stimulus offset by 3-4 cycles, even when signals are
 377 isolated from specific brain regions (Figure 3, second row). These techniques preclude the
 378 explanation that an apparent echo might be generated by signals with different degrees of lag
 379 summing within a scalp-recorded EEG signal (Coffey et al., 2021; Lerousseau et al., 2021). This
 380 finding represents evidence for entrainment echoes in the auditory system at higher frequencies,
 381 and demonstrates that FFR involves entrained neural oscillations.

382 3.3 Temporal dynamics of entrainment

383 By definition, neural entrainment occurs *during* stimulus processing. As such, it is important to
 384 identify the unique features of oscillatory dynamics in response to input that can both indicate its
 385 presence and affect downstream processing. For example, neural entrainment and stimulus-

386 evoked responses differ in how their temporal dynamics unfold. Whereas evoked responses are
 387 typically maximal at the onset of rhythmic stimulation and habituate subsequently, a neural
 388 oscillator might require some time to entrain to the stimulation (Figure 1d). Such an effect has
 389 been observed in epidural recordings from the prefrontal cortex of conscious rats during acoustic
 390 40-Hz stimulation (Figure 4), a “preferred” rate for auditory cortical circuits (Section 3.1). The
 391 onset of stimulation produced a strong evoked response that rapidly attenuated (Figure 4, top
 392 panel), while the phase synchrony to the stimulus at ~40 Hz developed slowly over the course of
 393 hundreds of milliseconds (Figure 4, bottom panel, left; Ummear Raza et al., 2023; Gautam et al.,
 394 2024). Importantly, whereas evoked responses manifest in a comparable fashion in the primary
 395 auditory and the prefrontal cortices (Gautam et al., 2024), the development of the ~40-Hz phase
 396 synchrony in the prefrontal cortex lagged markedly behind the former. Therefore, the slow
 397 evolution in phase synchrony appears to reflect a property underlying oscillatory circuitry.
 398 Interestingly, temporal phase dynamics and performance can vary between driving frequency and
 399 harmonics (Gautam et al., 2023; Swerdlow et al., 2024), suggesting the presence of multiple and
 400 divergent rhythm-sensitive networks. For example, in the rodent prefrontal cortex, while robust
 401 evoked responses were noted to click trains at 10, 20 and 40 Hz, strong synchrony emerged only
 402 at ~ 40 Hz.

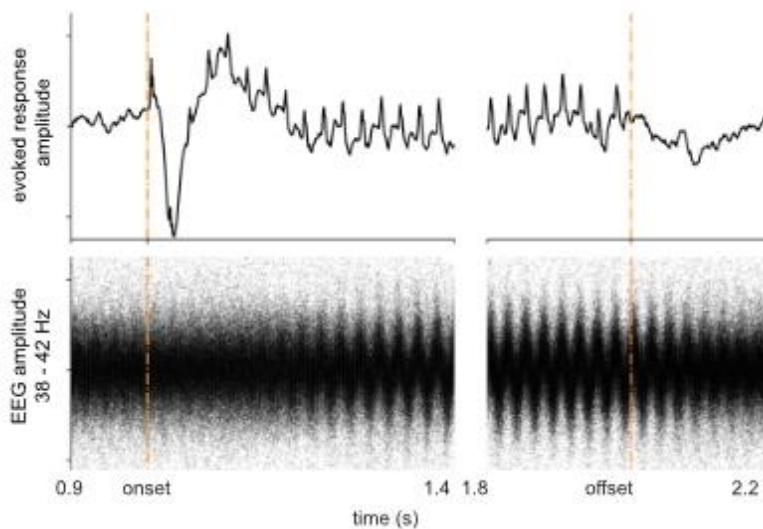


Figure 4. Top panel. An epidurally recorded prefrontal 40 Hz auditory steady state response (ASSR) averaged from a group of 11 female SD rats. Vertical lines mark stimulus period. **Bottom panel.** The single EEG epochs used to generate the 40 Hz ASSR (top panel) were band pass (38-42 Hz) filtered and overlaid to highlight the evolution of 40 Hz synchrony. Note the delayed emergence of 40 Hz synchrony.

Ross and colleagues were the first to highlight the temporal divergence between evoked responses and phase synchrony

419 at 40 Hz in human volunteers (Ross et al., 2002). They speculated that delayed phase synchrony
 420 may be indexing a higher order function such as temporal integration. Integrating discrete stimuli
 421 over time may subserve functions like pattern recognition and predictive coding (Fuster, 2001;
 422 Wolff et al., 2022). Since it takes 200-300 ms for gamma phase synchrony to establish in the
 423 prefrontal cortex in response to 40 Hz click trains, it is speculated that a minimum of 8-12 clicks
 424 may be necessary for rhythm registration in this paradigm.

425 The FFR, described in Section 3.2, can also be distinguished as oscillatory through other features
 426 of its temporal dynamics (Coffey et al., 2021; Figure 3). First, similar to the response to 40-Hz
 427 stimulation in rodents (Figure 4), FFR amplitude increases over time, peaking after several cycles
 428 of input (Figure 3, third row). Furthermore, frequency-tracking analysis, in which the fundamental
 429 frequency of successive overlapping windows is extracted and then plotted over the course of the

430 stimulus, revealed that despite the stimulus having a static fundamental frequency of 98 Hz, the
431 FFR appeared to converge to the stimulation frequency and then diverge once again following
432 stimulus offset, as expected from an entrained oscillator with a preferred frequency at about 80
433 Hz (Figure 3, fourth row; cf. Figure 2b). This pattern was most pronounced in data extracted from
434 the auditory cortex, whereas FFR generators located in the thalamus and below tended to show
435 tracking frequencies that better matched those of the incoming stimulus, also pointing to a specific
436 neural origin of auditory pitch-related oscillatory entrainment. In a separate experiment, responses
437 were measured to stimuli that were directly preceded by stimuli with higher or lower pitches in a
438 random stream. The results suggested that the frequency of the previous stimulus affects the
439 amplitude and frequency of the subsequently presented stimulus for several cycles.

440 Together, the temporal dynamics of the neural response during rhythmic stimulation begin to be
441 understood and entail positive evidence for endogenous oscillations in dynamic sensory
442 processing in the cases studied here. These oscillation-specific dynamics seem to occur at
443 frequencies that resemble “preferred” ones for oscillatory circuits, converging with approaches
444 described in Section 3.1 (see also Kaya and Henry, 2022, for a paradigm that combines the
445 oscillator’s preferred rate with its ability to adapt to sensory input). A focus on the temporal
446 evolution of neural dynamics can reveal entrained oscillations even when they cannot be
447 measured in the absence of stimulation.

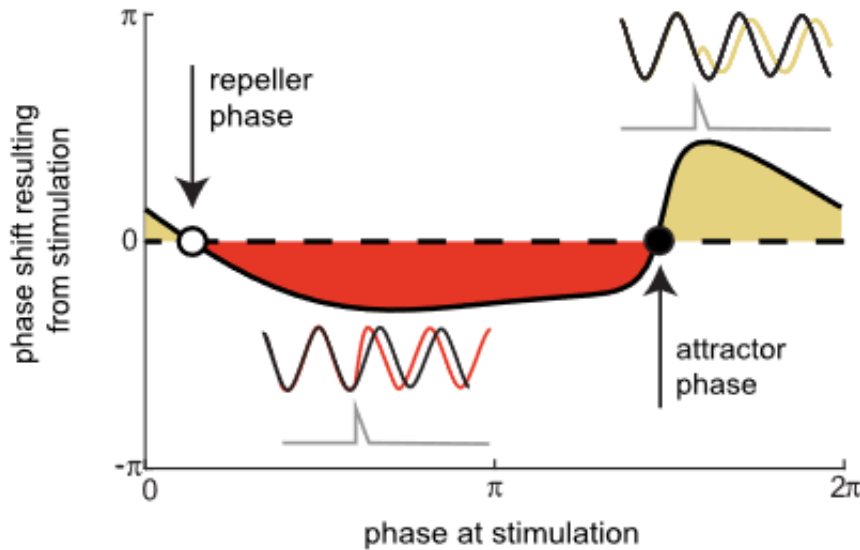
448 3.4 Modeling phase dynamics during rhythmic stimulation

449 One of the key drivers of oscillator utility is the ability to reduce the behavior of complex networks
450 as governed by a single variable, its phase. Pushing a pendulum in one direction at a particular
451 phase will increase its speed, at another phase it will reduce it (Figure 5). These phase dynamics
452 are critical not only towards identifying an oscillatory entrainment but also towards the theoretical
453 utility of this process in temporal cognition, like parsing and prediction. For this reason, it is critical
454 to identify how entrainment may differ from alternative sources of synchrony and what function
455 this may supply to downstream processing. An important approach to this end has been the
456 careful study of competing computational models and their comparison with both
457 neurophysiological and behavioral data.

458
459 Doelling et al., (2019) established this approach in music perception, highlighting that theories of
460 entrainment to support either auditory segmentation (Giraud and Poeppel, 2012) or prediction
461 (Arnal et al., 2015; Morillon et al., 2016) require a relatively consistent phase relationship with the
462 stimulus to be effective, regardless of stimulus rate. They compared an oscillator against a linear
463 response model in their phase consistency to music across a range of note rates. In doing so,
464 they found that MEG data of participants listening to the same music had higher phase
465 concentration, in line with the oscillator model. The results were consistent across two
466 experiments and three sets of musical pieces. These findings supported an oscillatory
467 entrainment hypothesis in the prediction of musical notes in natural music.

468
469 The FFR has also been modelled as a canonical model of mode-locked neural oscillations, which
470 do successfully predict the nonlinear responses to musical intervals observed in human data

471 (Lerud et al., 2014). However, evoked response models (Bidelman, 2015), and feed-forward delay
472 models (Tichko & Skoe, 2017) are also generally effective at producing signals that closely
473 resemble recorded FFRs.



494 **Figure 5.** Phase dynamics during stimulation is a key feature of oscillatory entrainment. The panel plots
495 the phase response curve of a nonlinear neural mass model oscillator (Wilson & Cowan, 1972) when
496 receiving pulsatile stimuli. The model's response (whether it lags or advances and by how much) to pulsatile
497 stimulation depends on the phase at which the stimulation occurs with one regime that causes phase lags
498 (yellow) and another that causes phase advancement (red). This leads to interesting dynamics when scaled
499 to sequences of stimulation: two "null phases" which have zero phase shift when stimulated, one an
500 attractor (filled circle), one a repeller (unfilled circle). These dynamics drive synchrony towards the attractor
501 phase and are a defining feature of oscillatory function. By modeling the phase dynamics of neural
502 recordings we can begin to distinguish dynamics of oscillatory and non-oscillatory sources in the brain.

504 More recently, Doelling and colleagues (2023) examined corresponding effects on behavior. They
505 studied a temporal prediction task in an "imprecisely isochronous" sequence of tones, where the
506 interval between tone onsets is normally distributed and centered on a specific period, akin to
507 syllable durations in speech. They found that participants behaved in accordance with Bayesian
508 principles, showing evidence for a prior expectation for rhythmicity in sequences. They tested a
509 number of mechanistic models to replicate this behavior, a simple ramp, a predictive ramp (Egger
510 et al., 2020), a nonlinear oscillator (Wilson and Cowan, 1972), and an adaptive frequency
511 oscillator (AFO). They found that only the two oscillator models could support this Bayesian prior
512 for rhythmicity, and only the AFO could do so at the range of rates reflected in experimental data
513 (1-5 Hz). This capacity to mimic Bayesian computation comes from the phase response curve of
514 the oscillator which is demonstrated in Figure 5 (see caption). This study has two key findings: 1)
515 entrainment biases perception towards rhythmicity, imposing rhythmic structure on perception, 2)
516 the base form of a nonlinear oscillator is too simple to support perception; added (non-oscillatory)
517 components support oscillatory dynamics to extend their utility to a wider range of stimuli.

518
519

520 3.5 Ruling out alternative mechanisms through study of selective 521 neuropsychological impairments

522 In some cases, it is difficult to attribute neural dynamics during stream presentation to oscillatory
523 entrainment or other processes, even using computational models. For example, as rhythms
524 inherently consist of concatenated intervals, it is not possible to design a periodic stimulus that
525 would not contain interval information. In such cases, even subtraction of a control condition (e.g.
526 aperiodic intervals; Breska and Deouell, 2017b) may not be sufficient, as it is difficult to determine
527 whether neural patterns that are specific to periodic stimulation do not reflect facilitated operation
528 of interval prediction mechanisms.

529 A unique solution for this challenge is offered by studying neurological patients, specifically with
530 cerebellar dysfunction (CD). While the cerebellum has traditionally been considered part of the
531 motor system, modern research has implicated it in high cognitive functions (Sokolov et al., 2017),
532 and, relevant here, in timing and temporal prediction. Critically, recent behavioral work has shown
533 that CD patients are selectively impaired in interval timing and prediction, and not in rhythm-based
534 timing (Grube et al., 2010; Breska and Ivry, 2018, 2021). Therefore, CD patients enable studying
535 entrainment during periodic stimulation while ascertaining that interval-based mechanisms are
536 not involved or explain neural dynamics. In a first study that applied this rationale, Breska & Ivry
537 (Breska and Ivry, 2020) measured EEG in CD patients and age-matched neurotypical controls.
538 They first verified that CD patients were impaired in interval-based temporal prediction, and
539 indeed found reduced levels of phase alignment at the stimulus frequency relative to controls, as
540 well as reduced behavioral benefit of predictive interval cues. Then, they showed that in a periodic
541 condition, CD patients showed similar degree of phase alignment as controls, which was also
542 stronger than the patients' phase alignment in interval prediction. These findings establish that
543 phase alignment during periodic stimulation does reflect rhythm-specific oscillatory mechanisms,
544 rather than interval prediction (Breska and Ivry, 2020).

545

546 4. Conclusion

547 Is an oscillator a useful model for how neural circuits respond to rhythmic stimulation? As we have
548 shown, the answer to this question strongly depends on the cognitive task, sensory domain, and
549 investigated neural mechanism. Our survey has found evidence for and against neural
550 entrainment as defined as neural oscillations phase-locked to sensory rhythms. While oscillations
551 are ubiquitous in extracellular and non-invasive brain recordings, their underlying generators likely
552 arise from an array of distinct mechanisms, some of which behave like physical oscillators, and
553 some do not. Moreover, oscillatory dynamics represent only one tool in the arsenal of neural
554 dynamics deployed by the brain to support perception and cognition. It therefore behooves us as
555 researchers to consider how such oscillations interact with other non-oscillatory components to
556 support cognition, to better understand where they can be useful and where they should be left
557 to the side. One consequence of this conclusion is that oscillator models of neural circuits should

558 be informed by the known properties of neurophysiological mechanisms (Figure 1e). For instance,
559 the ability of a stimulus to entrain endogenous oscillations will depend on its frequency and/or the
560 neural circuitry underlying the oscillation. As such, asking whether an oscillator is a useful model
561 to describe neuronal oscillations is too simplistic, as the answer depends on the complex
562 combination of parameters of the investigated circuit. Addressing the challenges described here
563 will bring us closer to understanding neural rhythms and their role in the processing of sensory
564 ones.

565

566 5. References

- 567 Adrian ED, Matthews BHC (1934) The Berger Rhythm: Potential changes from the occipital lobes in man.
568 *Brain* 57:355–385.
- 569 Arnal LH (2012) Predicting “When” Using the Motor System’s Beta-Band Oscillations. *Front Hum*
570 *Neurosci* 6.
- 571 Arnal LH, Doelling KB, Poeppel D (2015) Delta–Beta Coupled Oscillations Underlie Temporal Prediction
572 Accuracy. *Cereb Cortex* 25:3077–3085.
- 573 Barone J, Rossiter HE (2021) Understanding the Role of Sensorimotor Beta Oscillations. *Front Syst*
574 *Neurosci* 15.
- 575 Başar E (2013) Brain oscillations in neuropsychiatric disease. *Dialogues Clin Neurosci* 15:291–300.
- 576 Bidelman GM (2015) Multichannel recordings of the human brainstem frequency-following response:
577 Scalp topography, source generators, and distinctions from the transient ABR. *Hear Res* 323:68–
578 80.
- 579 Bittman EL (2021) Entrainment Is NOT Synchronization: An Important Distinction and Its Implications. *J*
580 *Biol Rhythms* 36:196–199.
- 581 Breska A, Deouell LY (2017a) Dance to the rhythm, cautiously: Isolating unique indicators of oscillatory
582 entrainment. *PLOS Biol* 15:e2003534.
- 583 Breska A, Deouell LY (2017b) Neural mechanisms of rhythm-based temporal prediction: Delta phase-
584 locking reflects temporal predictability but not rhythmic entrainment. *PLOS Biol* 15:e2001665.
- 585 Breska A, Ivry RB (2018) Double dissociation of single-interval and rhythmic temporal prediction in
586 cerebellar degeneration and Parkinson’s disease. *Proc Natl Acad Sci* 115:12283–12288.
- 587 Breska A, Ivry RB (2020) Context-specific control over the neural dynamics of temporal attention by the
588 human cerebellum. *Sci Adv* 6:eabb1141.
- 589 Breska A, Ivry RB (2021) The human cerebellum is essential for modulating perceptual sensitivity based
590 on temporal expectations Baker CI, Carrasco M, van Ede F, eds. *eLife* 10:e66743.
- 591 Bressler SL, Kelso JAS (2001) Cortical coordination dynamics and cognition. *Trends Cogn Sci* 5:26–36.
- 592 Brugge JF, Nourski KV, Oya H, Reale RA, Kawasaki H, Steinschneider M, Howard MA (2009) Coding of
593 repetitive transients by auditory cortex on Heschl’s gyrus. *J Neurophysiol* 102:2358–2374.
- 594 Buzsáki G, Draguhn A (2004) Neuronal oscillations in cortical networks. *Science* 304:1926–1929.
- 595 Buzsáki G, Logothetis N, Singer W (2013) Scaling Brain Size, Keeping Timing: Evolutionary Preservation
596 of Brain Rhythms. *Neuron* 80:751–764.
- 597 Buzsáki G, Vöröslakos M (2023) Brain rhythms have come of age. *Neuron* 111:922–926.
- 598 Buzsáki G, Wang X-J (2012) Mechanisms of Gamma Oscillations. *Annu Rev Neurosci* 35:203–225.
- 599 Christian KM, Thompson RF (2003) Neural Substrates of Eyeblink Conditioning: Acquisition and
600 Retention. *Learn Mem* 10:427–455.
- 601 Coffey EBJ, Arseneau-Bruneau I, Zhang X, Baillet S, Zatorre RJ (2021) Oscillatory Entrainment of the
602 Frequency-following Response in Auditory Cortical and Subcortical Structures. *J Neurosci*
603 41:4073–4087.
- 604 Coffey EBJ, Herholz SC, Chepesiuk AMP, Baillet S, Zatorre RJ (2016) Cortical contributions to the
605 auditory frequency-following response revealed by MEG. *Nat Commun* 7:11070.

606 Coffey EBJ, Nicol T, White-Schwoch T, Chandrasekaran B, Krizman J, Skoe E, Zatorre RJ, Kraus N
607 (2019) Evolving perspectives on the sources of the frequency-following response. *Nat Commun*
608 10:5036.

609 Connelly WM, Laing M, Errington AC, Crunelli V (2016) The Thalamus as a Low Pass Filter: Filtering at
610 the Cellular Level does Not Equate with Filtering at the Network Level. *Front Neural Circuits* 9.

611 Coull JT, Nobre AC (1998) Where and When to Pay Attention: The Neural Systems for Directing Attention
612 to Spatial Locations and to Time Intervals as Revealed by Both PET and fMRI. *J Neurosci*
613 18:7426–7435.

614 De Cheveigné A, Nelken I (2019) Filters: When, Why, and How (Not) to Use Them. *Neuron* 102:280–293.

615 De la Prida LM, Huberfeld G (2019) Inhibition and oscillations in the human brain tissue in vitro.
616 *Neurobiology of Disease* 125:198–210.

617 Doelling KB, Arnal LH, Assaneo MF (2023) Adaptive oscillators support Bayesian prediction in temporal
618 processing. *PLOS Comput Biol* 19:e1011669.

619 Doelling KB, Arnal LH, Ghitza O, Poeppel D (2014) Acoustic landmarks drive delta–theta oscillations to
620 enable speech comprehension by facilitating perceptual parsing. *NeuroImage* 85:761–768.

621 Doelling KB, Assaneo MF (2021) Neural oscillations are a start toward understanding brain activity rather
622 than the end. *PLOS Biol* 19:e3001234.

623 Doelling KB, Assaneo MF, Bevilacqua D, Pesaran B, Poeppel D (2019) An oscillator model better
624 predicts cortical entrainment to music. *Proc Natl Acad Sci* 116:10113–10121.

625 Drijvers L, Jensen O, Spaak E (2021) Rapid invisible frequency tagging reveals nonlinear integration of
626 auditory and visual information. *Hum Brain Mapp* 42:1138–1152.

627 Duecker K, Gutteling TP, Herrmann CS, Jensen O (2021) No Evidence for Entrainment: Endogenous
628 Gamma Oscillations and Rhythmic Flicker Responses Coexist in Visual Cortex. *J Neurosci*
629 41:6684–6698.

630 Edwards E, Chang EF (2013) Syllabic (~2-5 Hz) and fluctuation (~1-10 Hz) ranges in speech
631 and auditory processing. *Hear Res* 305:113–134.

632 Egger SW, Le NM, Jazayeri M (2020) A neural circuit model for human sensorimotor timing. *Nat Commun*
633 11:3933.

634 Farahbod H, Saberi K, Hickok G (2020) The rhythm of attention: Perceptual modulation via rhythmic
635 entrainment is lowpass and attention mediated. *Atten Percept Psychophys* 82:3558–3570.

636 Florez CM, McGinn RJ, Lukankin V, Marwa I, Sugumar S, Dian J, Hazrati L-N, Carlen PL, Zhang L,
637 Valiante TA (2015) In Vitro Recordings of Human Neocortical Oscillations. *Cerebral Cortex*
638 25:578–597.

639 Fries P (2015) Rhythms For Cognition: Communication Through Coherence. *Neuron* 88:220–235.

640 Fujioka T, Trainor LJ, Large EW, Ross B (2012) Internalized Timing of Isochronous Sounds Is
641 Represented in Neuromagnetic Beta Oscillations. *J Neurosci* 32:1791–1802.

642 Fuster JM (2001) The prefrontal cortex--an update: time is of the essence. *Neuron* 30:319–333.

643 Galambos R, Makeig S, Talmachoff PJ (1981) A 40-Hz auditory potential recorded from the human scalp.
644 *Proc Natl Acad Sci* 78:2643–2647.

645 Gautam D, Raza MU, Miyakoshi M, Molina JL, Joshi YB, Clayson PE, Light GA, Swerdlow NR, Sivarao
646 DV (2023) Click-train evoked steady state harmonic response as a novel pharmacodynamic
647 biomarker of cortical oscillatory synchrony. *Neuropharmacology* 240:109707.

648 Gautam D, Shields A, Krepps E, Ummear Raza M, Sivarao DV (2024) Click train elicited local gamma
649 synchrony: Differing performance and pharmacological responsivity of primary auditory and
650 prefrontal cortices. *Brain Res*:149091.

651 Giraud A-L, Poeppel D (2012) Cortical oscillations and speech processing: emerging computational
652 principles and operations. *Nat Neurosci* 15:511–517.

653 Gnanateja GN, Devaraju DS, Heyne M, Quique YM, Sitek KR, Tardif MC, Tessmer R, Dial HR (2022) On
654 the Role of Neural Oscillations Across Timescales in Speech and Music Processing. *Front*
655 *Comput Neurosci* 16.

656 Gray CM (1999) The Temporal Correlation Hypothesis of Visual Feature Integration: Still Alive and Well.
657 *Neuron* 24:31–47.

658 Greenfield MD, Merker B (2023) Coordinated rhythms in animal species, including humans: Entrainment
659 from bushcricket chorusing to the philharmonic orchestra. *Neurosci Biobehav Rev* 153:105382.

660 Griffiths BJ, Jensen O (2023) Gamma oscillations and episodic memory. *Trends Neurosci* 46:832–846.

661 Grube M, Cooper FE, Chinnery PF, Griffiths TD (2010) Dissociation of duration-based and beat-based
662 auditory timing in cerebellar degeneration. *Proc Natl Acad Sci* 107:11597–11601.

663 Haegens S, Zion Golumbic E (2018) Rhythmic facilitation of sensory processing: A critical review.
664 *Neurosci Biobehav Rev* 86:150–165.

665 Hanslmayr S, Matuschek J, Fellner M-C (2014) Entrainment of prefrontal beta oscillations induces an
666 endogenous echo and impairs memory formation. *Curr Biol* 24:904–909.

667 Hawken MJ, Shapley RM, Grosf DH (1996) Temporal-frequency selectivity in monkey visual cortex. *Vis*
668 *Neurosci* 13:477–492.

669 Helfrich RF, Breska A, Knight RT (2019) Neural entrainment and network resonance in support of top-
670 down guided attention. *Curr Opin Psychol* 29:82–89.

671 Henry MJ, Obleser J (2012) Frequency modulation entrains slow neural oscillations and optimizes human
672 listening behavior. *Proc Natl Acad Sci U S A* 109:20095–20100.

673 Herrmann CS (2001) Human EEG responses to 1-100 Hz flicker: resonance phenomena in visual cortex
674 and their potential correlation to cognitive phenomena. *Exp Brain Res* 137:346–353.

675 Herrmann CS, Rach S, Neuling T, Strüber D (2013) Transcranial alternating current stimulation: a review
676 of the underlying mechanisms and modulation of cognitive processes. *Front Hum Neurosci* 7.

677 Herweg NA, Solomon EA, Kahana MJ (2020) Theta Oscillations in Human Memory. *Trends Cogn Sci*
678 24:208–227.

679 Hickok G, Farahbod H, Saberi K (2015) The Rhythm of Perception: Entrainment to Acoustic Rhythms
680 Induces Subsequent Perceptual Oscillation. *Psychol Sci* 26:1006–1013.

681 Hoogenboom N, Schoffelen J-M, Oostenveld R, Parkes LM, Fries P (2006) Localizing human visual
682 gamma-band activity in frequency, time and space. *NeuroImage* 29:764–773.

683 Howard MW, Rizzuto DS, Caplan JB, Madsen JR, Lisman J, Aschenbrenner-Scheibe R, Schulze-
684 Bonhage A, Kahana MJ (2003) Gamma Oscillations Correlate with Working Memory Load in
685 Humans. *Cereb Cortex* 13:1369–1374.

686 Iaccarino HF, Singer AC, Martorell AJ, Rudenko A, Gao F, Gillingham TZ, Mathys H, Seo J, Kritskiy O,
687 Abdurrob F, Adaikkan C, Canter RG, Rueda R, Brown EN, Boyden ES, Tsai L-H (2016) Gamma
688 frequency entrainment attenuates amyloid load and modifies microglia. *Nature* 540:230–235.

689 Jacobs J (2014) Hippocampal theta oscillations are slower in humans than in rodents: implications for
690 models of spatial navigation and memory. *Philos Trans R Soc B Biol Sci* 369:20130304.

691 Javitt DC, Siegel SJ, Spencer KM, Mathalon DH, Hong LE, Martinez A, Ehlers CL, Abbas AI, Teichert T,
692 Lakatos P, Womelsdorf T (2020) A roadmap for development of neuro-oscillations as translational
693 biomarkers for treatment development in neuropsychopharmacology. *Neuropsychopharmacol*
694 45:1411–1422.

695 Jensen O (2024) Distractor inhibition by alpha oscillations is controlled by an indirect mechanism
696 governed by goal-relevant information. *Commun Psychol* 2:1–11.

697 Jensen O, Mazaheri A (2010) Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by
698 Inhibition. *Front Hum Neurosci* 4.

699 Jones SR (2016) When brain rhythms aren't "rhythmic": implication for their mechanisms and meaning.
700 *Curr Opin Neurobiol* 40:72–80.

701 Kaya E, Henry MJ (2022) Reliable estimation of internal oscillator properties from a novel, fast-paced
702 tapping paradigm. *Sci Rep* 12:20466.

703 Kazanina N, Tavano A (2023) What neural oscillations can and cannot do for syntactic structure building.
704 *Nat Rev Neurosci* 24:113–128.

705 Keitel C, Quigley C, Ruhnau P (2014) Stimulus-Driven Brain Oscillations in the Alpha Range: Entrainment
706 of Intrinsic Rhythms or Frequency-Following Response? *J Neurosci* 34:10137–10140.

707 Keitel C, Ruzzoli M, Dugué L, Busch NA, Benwell CSY (2022) Rhythms in cognition: The evidence
708 revisited. *Eur J Neurosci* 55:2991–3009.

709 Kimura M (1980) Neuronal responses of cat's striate cortex to flicker light stimulation. *Brain Res* 192:560–
710 563.

711 Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: The inhibition–timing hypothesis.
712 *Brain Res Rev* 53:63–88.

713 Lakatos P, Gross J, Thut G (2019) A New Unifying Account of the Roles of Neuronal Entrainment. *Curr*
714 *Biol CB* 29:R890–R905.

715 Lakatos P, Karmos G, Mehta AD, Ulbert I, Schroeder CE (2008) Entrainment of neuronal oscillations as a
716 mechanism of attentional selection. *Science* 320:110–113.

717 Leicht G, Vauth S, Polomac N, Andreou C, Rauh J, Mußmann M, Karow A, Mulert C (2016) EEG-
718 Informed fMRI Reveals a Disturbed Gamma-Band-Specific Network in Subjects at High Risk for
719 Psychosis. *Schizophr Bull* 42:239–249.

720 Lerousseau JP, Trébuchon A, Morillon B, Schön D (2021) Frequency Selectivity of Persistent Cortical
721 Oscillatory Responses to Auditory Rhythmic Stimulation. *J Neurosci* 41:7991–8006.

722 Lerud KD, Almonte FV, Kim JC, Large EW (2014) Mode-locking neurodynamics predict human auditory
723 brainstem responses to musical intervals. *Hear Res* 308:41–49.

724 L'Hermite S, Zoefel B (2023) Rhythmic Entrainment Echoes in Auditory Perception. *J Neurosci* 43:6667–
725 6678.

726 Lin WM, Oetinger DA, Bakker-Marshall I, Emmerzaal J, Wilsch A, ElShafei HA, Rassi E, Haegens S
727 (2022) No behavioural evidence for rhythmic facilitation of perceptual discrimination. *Eur J*
728 *Neurosci* 55:3352–3364.

729 Lisman JE, Jensen O (2013) The Theta-Gamma Neural Code. *Neuron* 77:1002–1016.

730 Luo H, Poeppel D (2007) Phase patterns of neuronal responses reliably discriminate speech in human
731 auditory cortex. *Neuron* 54:1001–1010.

732 Meyer L, Sun Y, Martin AE (2020) “Entraining” to speech, generating language? *Lang Cogn Neurosci*
733 35:1138–1148.

734 Minarik T, Berger B, Jensen O (2023) Optimal parameters for rapid (invisible) frequency tagging using
735 MEG. *NeuroImage* 281:120389.

736 Miniussi C, Wilding EL, Coull JT, Nobre AC (1999) Orienting attention in time: Modulation of brain
737 potentials. *Brain* 122:1507–1518.

738 Morillon B, Schroeder CE, Wyart V, Arnal LH (2016) Temporal Prediction in lieu of Periodic Stimulation. *J*
739 *Neurosci* 36:2342–2347.

740 Müller MM, Picton TW, Valdes-Sosa P, Riera J, Teder-Sälejärvi WA, Hillyard SA (1998) Effects of spatial
741 selective attention on the steady-state visual evoked potential in the 20–28 Hz range. *Cogn Brain*
742 *Res* 6:249–261.

743 Notbohm A, Kurths J, Herrmann CS (2016) Modification of Brain Oscillations via Rhythmic Light
744 Stimulation Provides Evidence for Entrainment but Not for Superposition of Event-Related
745 Responses. *Front Hum Neurosci* 10:10.

746 Obleser J, Kayser C (2019) Neural Entrainment and Attentional Selection in the Listening Brain. *Trends*
747 *Cogn Sci* 23:913–926.

748 Oganian Y, Kojima K, Breska A, Cai C, Findlay A, Chang E, Nagarajan SS (2023) Phase Alignment of
749 Low-Frequency Neural Activity to the Amplitude Envelope of Speech Reflects Evoked Responses
750 to Acoustic Edges, Not Oscillatory Entrainment. *J Neurosci* 43:3909–3921.

751 Pan Y, Frisson S, Jensen O (2021) Neural evidence for lexical parafoveal processing. *Nat Commun*
752 12:5234.

753 Peter A, Uran C, Klon-Lipok J, Roese R, van Stijn S, Barnes W, Dowdall JR, Singer W, Fries P, Vinck M
754 (2019) Surface color and predictability determine contextual modulation of V1 firing and gamma
755 oscillations Colgin L, ed. *eLife* 8:e42101.

756 Picton TW, Vajsar J, Rodriguez R, Campbell KB (1987) Reliability estimates for steady-state evoked
757 potentials. *Electroencephalogr Clin Neurophysiol Potentials Sect* 68:119–131.

758 Pikovsky A, Rosenblum M, Kurths J (2001) *Synchronization: A Universal Concept in Nonlinear Sciences*.
759 Cambridge: Cambridge University Press.

760 Poeppel D, Assaneo MF (2020) Speech rhythms and their neural foundations. *Nat Rev Neurosci* 21:322–
761 334.

762 Popov T, Szyszka P (2020) Alpha oscillations govern interhemispheric spike timing coordination in the
763 honey bee brain. *Proc R Soc B Biol Sci* 287:20200115.

764 Regan D (1966) Some characteristics of average steady-state and transient responses evoked by
765 modulated light. *Electroencephalogr Clin Neurophysiol* 20:238–248.

766 Rohenkohl G, Nobre AC (2011) Alpha Oscillations Related to Anticipatory Attention Follow Temporal
767 Expectations. *J Neurosci* 31:14076–14084.

768 Rojas DC, Wilson LB (2014) Gamma-band abnormalities as markers of autism spectrum disorders.
769 *Biomark Med* 8:353–368.

770 Ross B, Draganova R, Picton TW, Pantev C (2003) Frequency specificity of 40-Hz auditory steady-state
771 responses. *Hear Res* 186:57–68.

772 Ross B, Picton TW, Pantev C (2002) Temporal integration in the human auditory cortex as represented
773 by the development of the steady-state magnetic field. *Hear Res* 165:68–84.

774 Rudoler JH, Herweg NA, Kahana MJ (2023) Hippocampal Theta and Episodic Memory. *J Neurosci*
775 43:613–620.

776 Schneider M, Tzanou A, Uran C, Vinck M (2023) Cell-type-specific propagation of visual flicker. *Cell Rep*
777 42:112492.

778 Schroeder CE, Lakatos P (2009) Low-frequency neuronal oscillations as instruments of sensory
779 selection. *Trends Neurosci* 32:9–18.

780 Sivarao DV (2015) The 40-Hz auditory steady-state response: a selective biomarker for cortical NMDA
781 function. *Ann N Y Acad Sci* 1344:27–36.

782 Sokolov AA, Miall RC, Ivry RB (2017) The Cerebellum: Adaptive Prediction for Movement and Cognition.
783 *Trends Cogn Sci* 21:313–332.

784 Soula M, Martín-Ávila A, Zhang Y, Dhingra A, Nitzan N, Sadowski MJ, Gan W-B, Buzsáki G (2023) Forty-
785 hertz light stimulation does not entrain native gamma oscillations in Alzheimer’s disease model
786 mice. *Nat Neurosci* 26:570–578.

787 Spaak E, Lange FP de, Jensen O (2014) Local Entrainment of Alpha Oscillations by Visual Stimuli
788 Causes Cyclic Modulation of Perception. *J Neurosci* 34:3536–3544.

789 Strogatz SH (2019) *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry,*
790 *and Engineering*, 2nd ed. Boca Raton: CRC Press.

791 Sun Y, Michalareas G, Poeppel D (2022) The impact of phase entrainment on auditory detection is highly
792 variable: Revisiting a key finding. *Eur J Neurosci* 55:3373–3390.

793 Swerdlow NR, Gonzalez CE, Raza MU, Gautam D, Miyakoshi M, Clayson PE, Joshi YB, Molina JL,
794 Talledo J, Thomas ML, Light GA, Sivarao DV (2024) Effects of Memantine on the Auditory
795 Steady-State and Harmonic Responses to 40 Hz Stimulation Across Species. *Biol Psychiatry*
796 *Cogn Neurosci Neuroimaging* 9:346–355.

797 Ten Oever S, Titone L, te Rietmolen N, Martin AE (2024) Phase-dependent word perception emerges
798 from region-specific sensitivity to the statistics of language. *PNAS Proc Natl Acad Sci U S Am*
799 121.

800 Teng X, Poeppel D (2020) Theta and Gamma Bands Encode Acoustic Dynamics over Wide-Ranging
801 Timescales. *Cereb Cortex N Y N 1991* 30:2600–2614.

802 Teng X, Tian X, Rowland J, Poeppel D (2017) Concurrent temporal channels for auditory processing:
803 Oscillatory neural entrainment reveals segregation of function at different scales. *PLOS Biol*
804 15:e2000812.

805 Tichko P, Skoe E (2017) Frequency-dependent fine structure in the frequency-following response: The
806 byproduct of multiple generators. *Hear Res* 348:1–15.

807 Traub RD, Whittington MA, Stanford IM, Jefferys JGR (1996) A mechanism for generation of long-range
808 synchronous fast oscillations in the cortex. *Nature* 383:621–624.

809 Uhlhaas PJ, Roux F, Rodriguez E, Rotarska-Jagiela A, Singer W (2010) Neural synchrony and the
810 development of cortical networks. *Trends Cogn Sci* 14:72–80.

811 Uhlhaas PJ, Singer W (2006) Neural Synchrony in Brain Disorders: Relevance for Cognitive Dysfunctions
812 and Pathophysiology. *Neuron* 52:155–168.

813 Ummear Raza M, Gautam D, Rorie D, Sivarao DV (2023) Differential Effects of Clozapine and
814 Haloperidol on the 40 Hz Auditory Steady State Response-mediated Phase Resetting in the
815 Prefrontal Cortex of the Female Sprague Dawley Rat. *Schizophr Bull* 49:581–591.

816 van Bree S, Alamia A, Zoefel B (2022) Oscillation or not-Why we can and need to know (commentary on
817 Doelling and Assaneo, 2021). *Eur J Neurosci* 55:201–204.

818 van Bree S, Sohoglu E, Davis MH, Zoefel B (2021) Sustained neural rhythms reveal endogenous
819 oscillations supporting speech perception. *PLOS Biol* 19:e3001142.

820 van Nifferick AM, Mulder D, Duineveld DJ, Diachenko M, Scheltens P, Stam CJ, van Kesteren RE,
821 Linkenkaer-Hansen K, Hillebrand A, Gouw AA (2023) Resting-state oscillations reveal disturbed
822 excitation–inhibition ratio in Alzheimer’s disease patients. *Sci Rep* 13:7419.

823 van Pelt S, Boomsma DI, Fries P (2012) Magnetoencephalography in Twins Reveals a Strong Genetic
824 Determination of the Peak Frequency of Visually Induced Gamma-Band Synchronization. *J*
825 *Neurosci* 32:3388–3392.

826 Vinck M, Uran C, Spyropoulos G, Onorato I, Brogginini AC, Schneider M, Canales-Johnson A (2023)
827 Principles of large-scale neural interactions. *Neuron* 111:987–1002.

828 Walter VJ, Walter WG (1949) The central effects of rhythmic sensory stimulation. *Electroencephalogr Clin*
829 *Neurophysiol* 1:57–86.

830 Weisz N, Lithari C (2017) Amplitude modulation rate dependent topographic organization of the auditory
831 steady-state response in human auditory cortex. *Hearing Research* 354:102–108.

832 Wilson HR, Cowan JD (1972) Excitatory and Inhibitory Interactions in Localized Populations of Model
833 Neurons. *Biophys J* 12:1–24.

834 Wolff A, Berberian N, Golesorkhi M, Gomez-Pilar J, Zilio F, Northoff G (2022) Intrinsic neural timescales:
835 temporal integration and segregation. *Trends Cogn Sci* 26:159–173.

836 Zhigalov A, Duecker K, Jensen O (2021) The visual cortex produces gamma band echo in response to
837 broadband visual flicker. *PLoS Comput Biol* 17:e1009046.

838 Zhigalov A, Herring JD, Herpers J, Bergmann TO, Jensen O (2019) Probing cortical excitability using
839 rapid frequency tagging. *NeuroImage* 195:59–66.

840 Zoefel B (2018) Speech Entrainment: Rhythmic Predictions Carried by Neural Oscillations. *Curr Biol*
841 28:R1102–R1104.

842 Zoefel B, Abbasi O, Gross J, Kotz SA (2024) Entrainment echoes in the cerebellum. *BioRxiv*, doi:
843 <https://doi.org/10.1101/2024.03.06.583255>

844 Zoefel B, Kösem A (2024) Neural tracking of continuous acoustics: properties, speech-specificity and
845 open questions. *Eur J Neurosci* 59:394–414.

846 Zoefel B, ten Oever S, Sack AT (2018) The Involvement of Endogenous Neural Oscillations in the
847 Processing of Rhythmic Input: More Than a Regular Repetition of Evoked Neural Responses.
848 *Front Neurosci* 12.

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