

A New Unifying Account of the Roles of Neuronal Entrainment

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Rhythms are a fundamental and defining feature of neuronal activity in animals including humans. This rhythmic brain activity interacts in complex ways with rhythms in the internal and external environment through the phenomenon of ‘neuronal entrainment’, which is attracting increasing attention due to its suggested role in a multitude of sensory and cognitive processes. Some senses, such as touch and vision, sample the environment rhythmically, while others, like audition, are faced with mostly rhythmic inputs. Entrainment couples rhythmic brain activity to external and internal rhythmic events, serving fine-grained routing and modulation of external and internal signals across multiple spatial and temporal hierarchies. This interaction between a brain and its environment can be experimentally investigated and even modified by rhythmic sensory stimuli or invasive and non-invasive neuromodulation techniques. We provide a comprehensive overview of the topic and propose a theoretical framework of how neuronal entrainment dynamically structures information from incoming neuronal, bodily and environmental sources. We discuss the different types of neuronal entrainment, the conceptual advances in the field, and converging evidence for general principles.

Introduction

Rhythmicity is an important feature of living organisms, as one of their fundamental properties is recurrent periods of activity and rest [1]. This leads to rhythmic patterns of activity, often controlled by brain rhythms. Examples are the sleep–wake cycles, the recurrent patterns of breathing or the coordinated activity of agonist and antagonist muscles during complex motor acts such as locomotion or speech [2]. But sensory processes have also been found to be rhythmic. There is evidence that animals and humans sense the environment in snapshots, rather than continuously, with the brain rhythms of enhanced sensitivity to sensory input cycling at specific frequencies [3]. While the rhythms of the motor system generate outputs that are of likely relevance for other organisms — for example, rhythmic patterns may signal an approaching predator or a conspecific trying to communicate — the rhythms of the sensory system facilitate the sampling of such information. Interestingly, the rhythms of motor production and sensory perception often match in intrinsic frequencies, which facilitates coupling between them. Examples are common frequencies involved in sound production and auditory sampling during speech [4–7], or in oculomotor [8], attentional scanning [9–11] and visual sampling [12,13] during active exploration of the environment. These frequencies are reflected in oscillations of the underlying neural systems, and are determined by physiological constraints of the generating elements, such as their microscopic and macroscopic structure (circuit and network architecture) and underlying time constants of synaptic connections [14,15]. Of note, the frequency of some neuronal oscillations has been kept constant through evolution despite changing brain size [16], indicating a functional importance for certain timescales.

While rhythmicity is an important feature of living organisms and their environment, entrainment enables the coordination of rhythmic activity between them. Entrainment is defined as the alignment of one or more oscillating systems to an external rhythm, whereby the interactions are unidirectional, that is, the external rhythm influences the oscillating system(s) but not *vice versa* (Figure 1A,B). The entrained oscillating system becomes enslaved by the rhythm of the driving force, and the two rhythms become effectively coupled. This contrasts with bidirectional coupling of oscillators, termed synchronization, which in the brain is thought to reflect essential network activity [17] (Figure 1C). For a brief introduction to the definition of entrainment within oscillation theory see Figure 1 and Box 1.

In physiological systems, entrainment enables or disables communication between two systems through aligning the receiver’s activity with the sender’s activity at specific phase delays and has been shown to be important across many levels of description. At the level of the organism, for example, entrainment to the slow circadian rhythm of light–dark (day–night) reversals enables organized activities in groups: de-synchronization of these rhythms across organisms would be very disruptive for cooperation. Still at the level of organisms, but at much higher frequencies, namely in the delta-to-theta frequency ranges [4,5,7,18], entrainment has been shown to be important for communication through speech [6,19]. Here, rhythmic sensing of speech sounds by a receiver aligns to the rhythmic patterns of auditory inputs that are produced by the motor speech areas of the sender. As for the slower circadian rhythms, perturbing this rhythmicity, for instance by presenting speech outside the natural rhythm, interferes with entrainment between the external driving force (the speech rhythm) and the receiver’s sensory



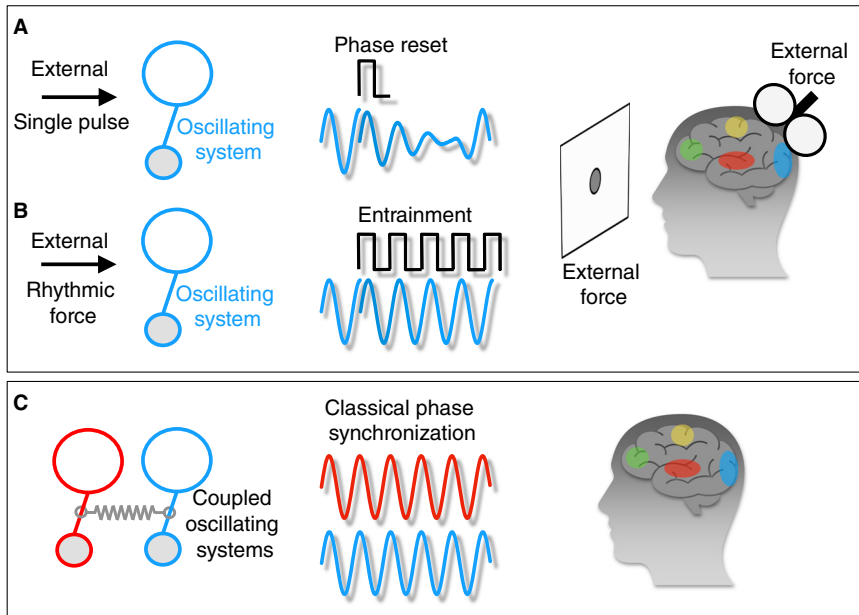


Figure 1. Phase reset vs. entrainment versus coupled oscillations (see also Box 1). (A) Phase reset by a single external event. Phase reset refers to the phase modulation of an oscillating system (brain rhythm) whereby a single event that is external to the oscillating system (for example, sensory input to cortex) forces the oscillating system into a specific phase at the time point of its occurrence. In the absence of repeated input (occurrence of one single event), however, the oscillation slowly reverts to its Eigen-dynamics, as illustrated. (B) Entrainment by rhythmic events external to an oscillating system. External rhythmic events result in wavelength modulation and amplitude stabilization of the oscillating system through a series of rhythmic (or quasi-rhythmic) phase-resets (see panel A). The wavelength is modulated to match the period of rhythmic input sequences that sequentially reset the phase of oscillations. (C) Phase synchronization of coupled oscillators. This is the result of weak bi-directional coupling of two self-sustained oscillators, which is different from the unidirectional mechanism of entrainment. While theoretically the distinction is clear cut, trying to isolate these mechanisms in the brain might pose significant signal processing challenges.

Current Biology

speech signals [20] and in turn reduces speech intelligibility [18,21–23]. Hence, entrainment facilitates optimal communication through aligning the rhythms of perception and production (or of the sensory and motor systems) across individuals. As a final example, entrainment can also disable the flow of incoming information. Rhythmic activity can be irrelevant for an organism — for example, dripping water, or even self-produced speech — in which case entrainment can be used to decouple the receiver from the rhythmic input stream.

Entrainment implies the presence of sequential (rhythmic) events. The latter are by themselves associated with some degree of predictability. Accordingly, entrainment helps efficient receiver–sender coordination by aligning relevant processes on the receiver’s end to predictable events produced on the sender’s end, with a possible net ethological advantage. Already 150 years ago Helmholtz pointed out the importance of predictive mechanisms in neuronal computations, arguing that one of the main operations our brain continuously performs is forming predictions about features of upcoming sensory and motor events [24]. Yet, research on these predictive mechanisms has only unfolded over the last two decades, providing a lot of evidence on their existence, neuronal substrates and function. The accumulated data come from a wide range of experiments and paradigms that studied different sensory modalities in several species including humans and non-human primates (for example [25–40]).

Several common themes emerged from these studies. First, purported predictive mechanisms engage the brain’s perpetually ongoing neuronal activity to manipulate inputs that have predictable features, and second, if timing is one of the predictable features of stimuli — which is more often the case than not — predictive mechanisms utilize neuronal oscillations. Specifically, if sensory inputs or the sampling of the environment is rhythmic, the brain can align a neuronal oscillation whose frequency is the closest match to the temporal structure of inputs, thereby

providing a constant oscillatory phase at which inputs arrive. Because the phase of neuronal oscillations reflects a rhythmic fluctuation of neuronal excitability [14,41,42], entraining to sensory inputs is beneficial, as entrainment can stabilize and adjust the gain that will be applied to the inputs. In other words, entrainment can set an internal context for the modulation and interpretation of external sensory or internal content based on the brain’s goals and expectations.

In brief, rhythmicity is an important feature of organisms, and entrainment a ubiquitous process for coordination of oscillating systems between organisms and their environment. Indeed, much evidence for its relevance exists. This evidence and its underlying principles are the focus of this review. We will first survey the empirical evidence for neuronal entrainment and outline its different flavors (for recent reviews on entrainment with different emphases see [26,32,43–51]). Because of the diversity of the findings and the relevance of oscillatory entrainment to brain operations, we feel that it is time for devising a unifying theoretical framework of neuronal entrainment, which we lay out in the subsequent section. We have termed this new account of neuronal entrainment ‘dynamic information selection by entrainment’ (DISE), and explain how it builds on and relates to existing theories of network communication and the structuring of information. Our theoretical framework emphasizes the importance of considering the brain within a larger context, including the environment and the body. One of its central tenets is that the brain can set up its connectivity matrix via entrainment phases (in *versus* out of phase) in alignment with expected stimulus inputs to emphasize task-relevant elements so that information is effectively routed according to forward models. Finally, we end our review with considerations about ‘a world without entrainment’, in which we imagine how the brain would operate without entrainment, and where we also point out that we do not consider neuronal oscillatory entrainment as a one-size-fits-all solution to all systems and cognitive neuroscience.

Box 1. Definition of entrainment within oscillation theory.

Classical models of synchronization in physics and dynamic system theory provide useful definitions to disambiguate several related terms that are often used with similar meanings in the neuroscience literature, although denoting different phenomena: synchronization, entrainment, and resonance [200]. According to theory, classical phase synchronization originates from weak bidirectional coupling of two self-sustained oscillators (Figure 1C). Classical entrainment, on the other hand, is unidirectional and results from an external periodic force acting on one or many self-sustained oscillators (Figure 1B), by phase resetting these oscillators through the constituent pulses of the rhythmic input train (see Figure 1A for an illustration of phase resetting by one single pulse). Hence, while phase reset due to a single stimulus is not entrainment *per se*, it can lead to entrainment (for example, when this stimulus is followed by others). Resonance (not illustrated) originates from unidirectional coupling where the receiving system is not a self-sustained oscillator. While these are useful theoretical definitions, disambiguating them in complex systems (including the brain) is difficult. First, all three phenomena are characterized by phase locking of at least two time series. Second, pertaining to entrainment as the main topic of this review, complex systems show different flavors of entrainment with a different degree of conformity with the theoretical definition. Let us consider examples that sample the range of phenomena that we subsume under entrainment. Listening to a voice message leads to entrainment of brain rhythms in auditory (and other) brain areas. This is an example of a clear unidirectional coupling. However, the situation is more complex when speaking yourself, because your motor cortex and auditory cortex are phase locked to the rhythm of your speech. There is coupling from motor areas to auditory areas, but also feedback from auditory areas to motor areas. We would still consider this to be entrainment because the motor system is clearly the driver. In summary, for the purpose of this review, we define entrainment as phase locking resulting from (predominantly) unidirectional coupling. As to biophysical models, phase resetting is relatively well understood in individual neurons and small, isolated populations (for example [201]). It is unclear, however, how this generalizes to population-based phase resetting and entrainment, as far as we know. For models of phase-resetting and/or entrainment in specific cases, please see [202–204].

Flavors of Entrainment

As outlined above, entrainment is the alignment of ongoing neuronal activity to the temporal structure of external rhythmic input streams. Entrainment usually entails phase alignment of brain oscillations (phase entrainment), but can also present as the alignment of rhythmically generated oscillatory events or bursts. In this scenario, the rhythmic bursts may result from cross-frequency interactions through which the phase of lower frequency oscillations — entrained by external input streams — modulates the amplitude of higher frequency oscillations (phase-amplitude coupling of neuronal oscillations) [42,52–55]. Whatever the output measure — low frequency oscillations or high frequency bursts — there is a considerable amount of information on the types of rhythmic inputs that are able to entrain ongoing oscillatory activity. We differentiate between three categories of such external rhythmic events: first, environmental rhythms that are external and sensory; second, self-produced rhythms, which can be subdivided into voluntary rhythms that are mostly motor, such as eye movements, and involuntary rhythms that are autonomously regulated, such as gastric or heart rhythms; and third, rhythmic neuromodulation, as by transcranial (electro-magnetic) stimulation.

In its basic form, neuronal entrainment from environmental rhythmic events arises from inputs that directly reach the receptors, independently of intentional motor control, as is the case for most auditory input (except generated ones like speech or walking). On the other hand, environmental rhythmic events can also be associated with rhythmic motor sampling patterns, like saccades or sniffing. We have mounting evidence by now that, in this case, inputs related to the motor sampling pattern — rather than the accompanying sensory inputs — reset and entrain ongoing neuronal activity in sensory areas, a process that can be subsumed under active sensing [56]. One example is the oculomotor signals associated with environmental exploration entraining various brain regions for facilitating effective perceptual

processing at upcoming visual fixation positions [57–59], an example of neuronal entrainment by a voluntary self-produced rhythm. This contrasts with neuronal entrainment by involuntary self-produced rhythms controlled by the autonomic nervous system, such as those involved in breathing, heartbeat and digestive processes. Entrainment by inputs conveying internally generated information streams like connected memories or ‘trains of thought’ is also conceivable. While we acknowledge that the existence of this form of internal entrainment is highly speculative, there is some evidence that it does occur [60].

Finally, given the evidence for the ubiquitous presence of entrainment in the brain, researchers have started to explore the possibility of neuronal entrainment by rhythmic neuromodulation, with the goal of using entrainment as an experimental or therapeutic tool; to date mostly studied using rhythmic, non-invasive transcranial stimulation. Entrainment by the different categories of rhythmic events is further detailed below. One particular area of our everyday lives where many of the different forms of entrainment are at play is conversation or speech (Figure 2 and Box 2).

Entrainment by Voluntary Self-produced Rhythms

We use the term voluntary self-produced (active) rhythms to describe the rhythmic motor activity patterns that can entrain neuronal oscillations in sensory brain regions supporting active sensing [56]. The advantage of this form of phase reset and entrainment is that the desired phase of neuronal excitability fluctuations can be set by the corollary discharge from the motor command that generates a sensory sampling action (for example, a saccade), prior to the arrival of the sensory input. In other words, the brain is informed by the motor system that a sensory input is meant to arrive with a certain delay. The delay is likely conveyed by a phase shift that corresponds to the time between the motor command and the predicted arrival of the sensory input. Besides the motor-to-sensory delay, the phase to which the oscillations are reset/entrained is likely conveying predictions

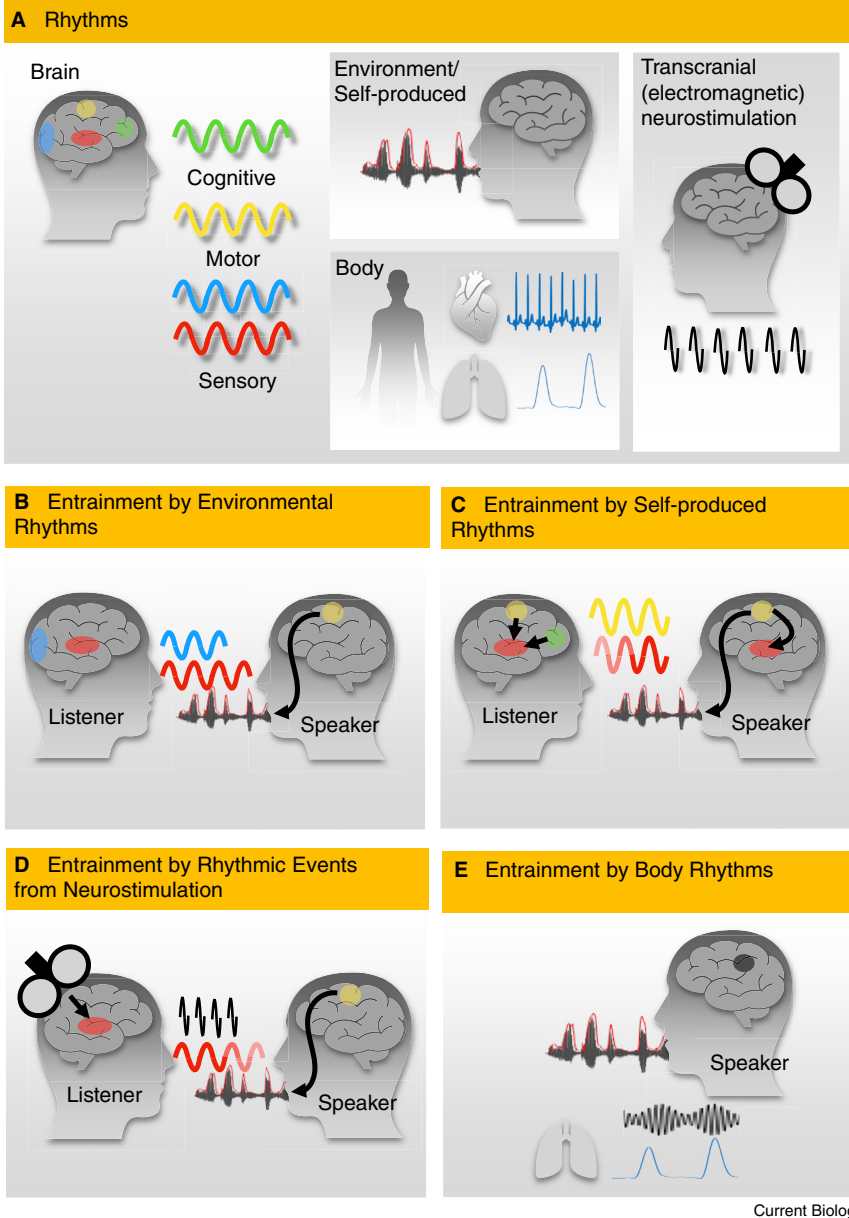


Figure 2. Schematic representation of different forms of entrainment during speech.

(A) Rhythms. Brain rhythms (left panel) and rhythmic forces that can entrain them (right panels), including environmental rhythms, self-produced (bodily) rhythms and rhythmic neuromodulation. (B–E) These panels expand on the distinct forms of entrainment with speech (conversation) as an example and underscore the main premise of our review that neuronal entrainment is ubiquitous in the brain and can be driven by very diverse rhythmic forces. (B) During a conversation, environmental sounds produced by a speaker entrain auditory cortex in the listener. (C) The associated motor speech production rhythms also lead to neuronal entrainment. (D) Entrainment by rhythmic neurostimulation. (E) Entrainment by body rhythms can also occur in the same setting. For a detailed description of the scenarios depicted in panels B–E, see [Box 2](#).

As a side note, the ‘disco experience’ is quite complex, as it involves audio-visual-somatosensory interactions, synchronized motor components and interpersonal interactions, all of which are likely mediated by oscillatory entrainment. Notably, while the disco experience that emphasizes synchrony [73,74] is distinct from the cocktail party experience, where asynchrony — the unique audiovisual rhythm of the attended speaker — plays a crucial role [75,76], both examples point to the importance of oscillatory entrainment in interpersonal interactions [77,78]. It is an unresolved question, however, whether the sensory inputs generated by rhythmic motor sampling patterns have a reciprocal effect on the motor system, or whether, along with motor inputs, they contribute to entrainment in sensory brain regions.

While in all of the above examples the role of voluntary self-produced rhythms is to enhance the sensing of behaviorally

relevant aspects of the external environment (active sensing), we suggest that self-produced rhythms can also be associated with the opposite — the suppression of self-generated sensory inputs, when related to one’s own rhythmic motor patterns (muffled sensing), because the latter are by definition behaviourally irrelevant. Examples for this are our own movements (walking) or vocalizations (speaking), which generate both rhythmic somatosensory and auditory (in the case of movement even visual) input patterns that are suppressed compared to when not self-generated [79–84]. There does seem to be emerging evidence for this suppressive form of entrainment (but see for example [85]).

about anticipated features of the to-be-sampled external objects, similar to entrainment during selective attention [61].

Obvious examples for neuronal entrainment by such voluntary self-produced rhythms are sniffing for olfaction [62–65], saccades (also termed visual sniffing by [66]) for vision [57–59,66], whisking or rubbing, which enhance somatosensory perceptual experience in rodents and primates, respectively [63,67], and finally licking, which enhances taste [68,69]. At first glance, it might appear that, because we do not rhythmically wiggle our ears in order to enhance sensing our auditory environment, audition is not supported by rhythmic motor sampling patterns. But recent research and a couple of real life experiences show that this is likely not the case: recent studies have found that rhythmic movement can facilitate auditory perception [70–72], which is likely why dancing enhances our musical experience at a disco.

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Entrainment by Involuntary Self-produced Rhythms

Entrainment research so far has largely focused on neuronal entrainment to rhythms in the external environment (such as

Box 2. Speech entrainment.

For humans, a highly relevant external sensory stimulus is speech (Figure 2). Interestingly, while speech is in principle continuous, meaningful entities are communicated at preferred rates. A notable example is the syllable that is typically produced at a rate of about five per second [4,5,7]. This typical rate therefore establishes a communication channel between interlocutors who can expect to receive syllables at this particular rate. This alignment [205] facilitates prediction as it establishes temporal synchrony between the speakers' and listeners' forward models.

Over recent years, many studies have monitored brain oscillations during continuous speech perception and provided converging evidence for entrainment. Speech entrainment is most strongly observed at frequencies below 10 Hz and is thought to result from phase resetting of ongoing oscillations in auditory cortex caused by rapid changes in the speech waveform (such as onsets) [6,206]. As a result of the phase resetting, brain activity will be temporally aligned to the quasi-rhythmic structure in speech, schematically represented in Figure 2B. This entrainment appears to be stronger for intelligible and attended speech [61,76,206–208]. A recent MEG study [209] could directly confirm a significantly stronger causal influence of higher-order brain areas (left inferior frontal gyrus and left motor areas) to auditory cortex for intelligible compared to unintelligible speech, suggesting an active component in neuronal entrainment by the environmental speech rhythms (Figure 2C). Building on [209], Assaneo and Poeppel [210] provided evidence that audio-motor interaction is restricted to a specific frequency range (~4.5 Hz), which supports the relevance of oscillations in audio-motor interactions. Similar 'top-down' entrainment involving the pulvinar, a high-order thalamic nucleus was observed in non-human primates in relation to complex repetitive acoustic patterns [36], which are important for speech perception and learning [211]. There is also evidence that listening performance can be enhanced by transcranial entrainment of auditory cortex through transcranial alternating current stimulation (tACS), if the tACS waveform is phase-lagged to the auditory (speech) input stream such that optimal tACS phase and input of salient events in the stream coincide [132,212] (Figure 2D). Finally, an example of body-brain entrainment during speech is the temporal adjustment of respiration and speech production (Figure 2E).

rhythmic sensory signals) ignoring the fact that the brain is part of the body. Importantly, there are continuous interactions between body and brain. The dynamically changing state of the body is partially controlled by the brain, while it in turn influences brain activity, affecting cognition and being altered in disease. In the context of entrainment, this is particularly relevant for rhythmic body signals that exist in different organs and span a wide range of frequencies [86]. Among body rhythms, the gastric basal rhythm can be recorded from the stomach and has a frequency of about 0.05 Hz [87]. Respiration has a typical frequency of ~0.25 Hz [88] and is an interesting case because it can be voluntarily controlled and needs to be temporally adjusted in many everyday tasks such as swallowing and speaking.

Unfortunately, we know relatively little about how these body rhythms interact with brain rhythms but there is some evidence for body-brain entrainment. It has been demonstrated with invasive recordings in mice that neuronal activity across many brain areas is temporally coupled to respiration [89,90]. This can be observed as phase locking at the frequency of respiration but also in the form of phase-amplitude coupling where the phase of respiration modulates the amplitude of oscillations at higher frequencies such as in the gamma band (80–150 Hz) [91,92]. In humans, respiratory-brain coupling is virtually unstudied, but two recent studies [93,94] using invasive recordings in epilepsy patients have demonstrated that brain oscillations at various frequencies can be locked to the respiratory cycle even in human non-olfactory brain areas. Zelano *et al.* [94] further demonstrated that the respiratory-brain coupling has behavioural consequences, as fear discrimination and memory retrieval are modulated by the phase of respiration. At a higher frequency of ~1 Hz, the heart beat is another body rhythm that is modulated by the brain (for example during states of fear) and that is also reflected in brain activity as heartbeat evoked brain responses that can be recorded with EEG and MEG [95,96].

While the heart has its own pacemaker, other bodily rhythms are imposed through (sometimes involuntary) rhythmic control of muscle movements such as in quasi-rhythmic saccades during free viewing [8] or slow precision movements [97] that operate in a frequency range of about 4–8 Hz. In these cases, the central control of rhythmic movements leads to self-generated rhythmic sensory input that can cause entrainment of rhythmic brain activity. Interestingly, brain responses to self-generated sensory input are typically attenuated [85,98–100], and as we discussed under voluntary self-produced rhythms, one conceivable mechanism is the entrainment of neuronal oscillations to their low excitability phases in order to suppress self-generated, possibly distracting inputs that have a predictable temporal pattern.

Entrainment by Rhythmic Neuromodulation

Given the evidence for functional relevance of entrainment, research has started to look into the potential of entraining the brain by non-invasive transcranial brain stimulation (NTBS) techniques, either as an experimental or a therapeutic tool [44,101,102]. Rhythmic forms of NTBS (rhNTBS), such as rhythmic transcranial magnetic stimulation (rhTMS) or transcranial alternating current stimulation (tACS), in particular, have been used to this end. These forms of stimulation are typically conceptualized as stimulating the brain directly (transcranially), although the electromagnetic stimuli applied on the scalp are often associated with peripheral sensations and therefore need to be sham-controlled to rule out indirect (sensory) stimulation effects. Such 'experimental' entrainment of brain oscillations allows establishing whether brain oscillations are causally driving brain function, as opposed to representing epiphenomenal activity, by examining its functional consequences [103]. With a causal link, entrainment of brain oscillations is also of interest as a therapeutic tool, given that several neurologic and psychiatric disorders are associated with specific oscillopathies [104–107].

Studying whether rhNTBS can be used for transcranial entrainment of brain activity requires the combination of rhNTBS techniques (rhTMS or tACS) with simultaneous (online) electrophysiological recordings (such as EEG or MEG). Computational modelling suggests that entrainment of brain activity by rhNTBS is feasible [108,109], at least for frequencies <50 Hz [109] and is likely state-dependent [110]. These modeling studies also mapped the input–response (NTBS-EEG) dynamics of entrainment, and showed that entrainment is hallmarked by enhanced likelihood of ‘resonance’ of oscillatory brain activity, if the stimulation frequency aligns with the natural frequency of the intrinsic oscillation. As a result, rhTMS and tACS entrainment designs tend to align the stimulation frequencies to the frequencies of the underlying brain oscillations.

What is the evidence for transcranial neuronal entrainment by rhNTBS? From simultaneous rhTMS-EEG studies in human participants, there is good evidence that one single TMS pulse phase resets ongoing brain oscillations, a prerequisite of entrainment [111], and that administering short bursts of TMS pulses at the frequency of the underlying brain oscillations entrains these oscillations [112–115], with some evidence that frequency-alignment to intrinsic oscillations facilitates entrainment [114]. These studies also provided evidence for brain oscillations being causally implicated in cognitive functions [113,115,116] and in driving excitability fluctuations [117]. For instance, rhTMS at alpha frequency over parietal areas causes visual perception to fluctuate in an alpha cycle, that is, to entrain at the alpha frequency [117]. Similarly, simultaneous tACS-EEG/MEG studies in human participants have presented evidence that tACS can entrain brain oscillations [118–120] (for evidence in other animals see [108,121,122]), again with consequences on associated sensory, motor, and cognitive functions (for example [123–126]). For instance, applying tACS at different frequencies over sensory or motor areas causes discrete sensory perception and motor excitability to entrain at the stimulation frequency (see for visual stimuli [118]; for tactile stimuli [127]; for sounds [128,129]; for motor cortex excitability [130]). Similarly, tACS of auditory areas benefits perception of serial auditory events if tACS is aligned in frequency and phase with the rhythmic input stream (for auditory streaming [131]; for speech [132,133]), which is in line with the idea that frequency of brain oscillations causally determines the rate of sensory sampling.

A note of caution is warranted, however. Recent studies using intracranial recordings in humans or animals simultaneously with tACS have raised concerns about the effect size of tACS on brain activity [134,135], suggesting that typically used tACS-intensities are likely at the lower end of what is required to affect the brain through the skull [136] (but see [137,138]). There are also concerns about residual, non-linear artefacts contaminating EEG/MEG-recordings during tACS, and hence about the quality of the data used to test tACS-entrainment in electrophysiological recordings [139–141] (see also [142]). Finally, next to the weak tACS effect size, there is evidence that peripheral sensations associated with tACS — such as touch and retinal phosphenes [143–145] — contribute to tACS entrainment effects indirectly via sensory entrainment [146]. Future rhNTBS studies will have to optimize stimulation protocols to enhance effect size, and also to more strictly compare the resulting entrainment effects to interventions with rhythmic photic, acoustic or tactile stimuli — to test the contribution of simple (indirect) sensory

entrainment to the observed rhNTBS entrainment effects [147,148].

Entrainment for Neuromodulation beyond Rhythmic Transcranial Stimulation

Rhythmic sensory stimuli themselves have been found to entrain brain oscillations, and this with behavioural consequences, for example, by causing fluctuations in perception, in a manner analogous to the rhNTBS-entrainment effects on perception outlined above (for visual stimuli [27,149–151]; for auditory stimuli [152–154]; for crossmodal stimuli [155]). Hence, sensory entrainment *per se* may show promise for experimental and possibly clinical use. Indeed, recent multisensory gamma entrainment in a mouse model of Alzheimer disease has demonstrated reduced amyloid levels and improved memory [156]. In humans, presenting sounds in-phase and at the frequency of slow-wave sleep enhances subsequent memory retrieval, likely through enhancing spindle activity-related memory consolidation via entraining slow-wave sleep [157,158]. And presenting simultaneous, amplitude-modulated audio-visual input streams (during wakefulness) at specific frequencies (theta) and phase-lags, such that activity in auditory and visual areas is synchronized, enhances the episodic (associative) memory for these audio-visual events [159,160]. Notably, the theta-specificity of these memory effects suggests that sensory entrainment reached downstream memory areas that are known to resonate at theta frequency, such as the hippocampus [159]. Hence, entrainment by external rhythmic stimulation may propagate beyond the input area (supramodality of entrainment) and holds promise as an experimental and clinical intervention tool irrespective of stimulus modality.

A Unifying Account of Neuronal Entrainment

Altogether the evidence discussed above indicates that neuronal entrainment is not solely a mechanism aiding processing of sensory information within the brain as it is often portrayed, but rather it is a fundamental mechanism that transcends supposedly distinct brain functions, pointing towards a more general purpose for coupling between internal and external elements. Below, we outline a new unifying account of the function that entrainment serves, and how entrainment mechanistically manipulates rhythmic inputs. The building blocks on which we base our account are outlined in **Box 3**, providing pointers to lines of research and open questions. We say that the account is unifying because it builds on and integrates existing theories of network communication and sensory sampling, and because it considers rhythmic brain activity within the wider context of a multitude of existing external rhythms. It shares features with the theories of communication through coherence [41,161], communication through resonance [162], active sensing [56], and dynamic attending [163,164]. It complements the theories of communication through coherence and communication through resonance by proposing that communication from the multitude of external rhythmic (and quasi-rhythmic) sources of information is engaged by entrainment, and adds an active and predictive component (as in active sensing and dynamic attending) which involves top-down control and expectations. We also incorporate novel evidence that brain operations can be influenced by self-generated movements and autonomous body functions, most of which are rhythmic/predictable. This is further detailed below. In the remainder of this section, we will

Box 3. Foundations of a theoretical, neuronal entrainment framework.

Much evidence for neuronal entrainment has been amassed in the past few decades. We feel that this constitutes a solid enough foundation upon which to build a useful theoretical (mechanistic) framework (see text). In this box, we define the building blocks of this framework, with the aim to help guiding research and point to open questions. We must emphasize that we do not suggest that all these building blocks will stand the test of time, but we do suggest that rather than gathering more incremental evidence for their existence, we should try to devise experiments that would unequivocally refute them, or shift our focus to explore further related issues that we will mention at the end of each paragraph in this box, if applicable.

- *Building block 1: entrainment exists.* While there are certain methodological caveats in demonstrating entrainment [213–216], the electrophysiological and behavioral data amassed using a wide range of stimuli and stimulation parameters leaves no doubt that neuronal entrainment exists in the brain, and that it has behavioral consequences [2,25–39]. Of note, a recent study [217] demonstrated in a rare, direct comparison that an oscillatory model outperforms an evoked model in explaining neuronal responses to rhythmic input.
- *Building block 2: function of entrainment.* Entrainment serves dynamic selection of information. The phase-specific alignment of ongoing brain rhythms to the temporal structure of input sequences by entrainment allows the brain to predict both their timing and features, in order to manipulate their processing according to current goals. While ‘network resonance’ [43] might contribute to some of the observed effects, like recruiting neuronal oscillations across distinct neuronal ensembles, it cannot explain feature-specific phase maps across topographically organized cortical regions established by neuronal entrainment [168], as resonance is not ‘phase specific’. These phase maps are set up by oscillations entrained to their high excitability phases only in regions processing relevant inputs, while coherent oscillations in all other regions are entrained to their opposing, low excitability phases. This amounts to a two-dimensional filter mechanism in the brain that filters sensory inputs along both the dimension of time, which is important for all senses, and a second dimension, which is topographically mapped and varies by sense, for example, frequency in the auditory domain or space in the somatosensory domain (see ‘unifying account of neuronal entrainment’ in the text and Figure 3).
- *Building block 3: mechanism of entrainment.* The mechanism of entrainment in the brain is a sequential phase modulation of ongoing oscillations by inputs, also termed phase reset [42,170, 203,218] (see also Box 1). Therefore, most properties of oscillatory entrainment extend to phase reset (most notably top-down modulation and supramodality, see below). An open question is how fast and to what degree oscillatory wavelength is adjusted by phase reset and adjunct mechanisms in order to match the period of input sequences [215].
- *Building block 4: specificity of entrainment.* Neuronal entrainment is not ‘frequency specific’. While there appear to be preferred frequencies, neuronal entrainment has been demonstrated in all ‘traditional’ frequency ranges (delta, theta, alpha, beta and gamma). An open question is whether, and to what degree, frequency specificity may be system or brain state specific [3,180,219,220].
- *Building block 5: entrainment is top-down controlled.* While the process of oscillatory alignment or entrainment can be automatic, it is under strong cognitive top-down control, at least in primates [35,149,188,220–223]. The influence of top-down control in modulating entrainment is probably greater in more developed, complex species [2], and in more crowded environments [222], albeit this has not been tested systematically. What is clear is that in primates, entrainment can be completely suppressed if a rhythmic stimulus stream is ignored [61,168], although this likely depends on the weight of sensory inputs (the sound of a jackhammer is harder to ignore than the ticking of a clock). We propose that entrainment operates on a similar basis as what is described as the capacity theory of attention [169], in that simultaneous input streams continuously compete for the supporting mechanisms (for example, phase reset), and the strongest input stream — after being weighted by top-down modulation — entrains oscillations. In other words, if there are only a few input streams present, they will likely all get a chance to entrain the brain at least for periods of time. However, in the presence of a lot of competing input streams, like at a cocktail party, the brain has to prioritize, and many rhythmic input streams will get shut out from gaining access to neuronal oscillations.
- *Building block 6: entrainment tolerates input variability.* Entrainment is tolerant to input timing variability [37,46,215,217], just as is human rhythm perception [224]. In other words, input sequences do not have to be completely predictable or isochronous in order to entrain brain rhythms and reap the benefits of entrainment, which makes it suitable to aid in the perception of quasi-rhythmic stimulus streams like speech for example, or quasi-rhythmic sampling of the sensory environment via saccades for example.
- *Building block 7: entrainment is supramodal.* Entrainment is supramodal, meaning that oscillations in one modality can be entrained by rhythmic inputs of any other modality [37,40,225,226]. This likely extends to higher order cortical structures being entrainable by external stimulus-related inputs and lower order sensory structures being entrainable by internal inputs related to e.g. memory recall, albeit this remains to be explored. The supramodality of entrainment ensures that timing of inputs in one sensory modality can guide ongoing oscillations in “extra-modal” brain regions, to aid in processing concurrent or subsequent inputs in other modalities, like during communication, where visual cues aid auditory perception [227].
- *Building block 8: entrainment is ubiquitous.* Our final building block is that entrainment can be established by a multitude of rhythmic inputs, including rhythmic sensory (environmental) inputs [37], by inputs related to self-produced rhythms such as those associated with active sensing (for example, saccades for vision, sniffing for olfaction and so on) [56], by rhythmic bodily

(Continued on next page)

Box 3. Continued

signals (for example, indexing autonomic rhythms like breathing [228]) and possibly also top-down inputs orchestrating internal information transfer [60,229]. If neuronal oscillations become entrained by any of these rhythms, this provides a central timing mechanism that other processes can align to. For example, when we tap to the rhythm of a song, motor signals responsible for orchestrating tapping are aligned to brainwaves entrained by auditory inputs. On the other hand, in the case of playing the piano, motor signals responsible for orchestrating tapping on the keys are entraining brainwaves that enhance auditory inputs generated by them. To summarize, if a temporal relationship exists between any of the sensory/motor/internal rhythms, there is likely to be an entraining input stream with the remaining temporally correlated inputs either enhanced or suppressed [230]. The entraining input stream is determined by an interaction of brain state including behavioral goals (motivation [231]), strength of the inputs (external environment), and the body (internal environment).

define neuronal entrainment from a mechanistic perspective, starting with the simplest, less debated functionality and ending with the most complex, more debated ones.

Local Excitability Effects

It is easy to argue that if neuronal entrainment serves a single function, it is *surely* the elimination of ‘random interference’ of ongoing oscillations with sensory or other inputs. A plethora of research demonstrates that neuronal oscillations reflect rhythmic changes of excitability and thereby change the weight of sensory input [14,41,42]. Therefore, without an alignment of neuronal oscillations to the timing of inputs from the sensory environment, or of inputs from other sources of information, neuronal oscillations would hinder the establishment of stable sensory or other representations, as they would amplify or attenuate information randomly, depending on which random oscillatory phase inputs arrive at. As we will describe later, this is not always a bad thing, as it can help ignoring certain inputs. But it would not serve the brain well if this scenario were to occur in relation to relevant inputs. Therefore, the brain’s strategy is to align neuronal oscillations to the timing of inputs for rhythmic sampling via neuronal entrainment to thereby eliminate variability.

An early proposed function for oscillatory entrainment was the amplification of inputs that occur at times predicted by the temporal structure of attended stimulus streams [165–167]. Later, electrophysiological studies provided evidence for this, and also demonstrated that the enhancement of attended rhythmic sensory inputs by the alignment of high excitability oscillatory phases is under strong top-down control: when streams of stimuli are attended, entrainment is stronger, while for ignored streams entrainment is weaker or does not occur at all [61,168]. Importantly, while some studies that observed entrainment did not control attention [36,42], it is conceivable that, as in these studies there was only one stimulus stream present in the environment, with minimal ‘competition’, this stream was able to entrain brain rhythms, in line with the capacity theory of attention [169]. Thus, observing entrainment in uncontrolled attentional states does not necessarily mean that entrainment is automatic, rather it means that the brain made no attempt to suppress it due to the availability of information processing ‘resources’.

Recently, it became clear that the amplification of attended sensory inputs by the alignment of high excitability phases is not the only type of input modulation that oscillatory entrainment is capable of. In the auditory domain, the phase of oscillatory entrainment by attended rhythmic stimulus streams creates a

two-dimensional phase map across tonotopically organized neuronal ensembles in primary auditory cortex (A1), where the phase of oscillations establishes a spatiotemporal ‘attentional spotlight’ across differently tuned A1 regions (Figure 3). If attention is directed towards a certain tone frequency, the region processing this frequency (the spotlight region) is entrained to its high excitability phase, while regions that process non-attended frequencies are entrained to their low excitability phases [61,168]. This creates the above mentioned two-dimensional, spatiotemporal phase or excitability map, which ensures that at attended time points, only attended frequency content is amplified, while other frequency content is suppressed (Figure 3).

We propose that the same spatiotemporal entrainment mechanism operates in topographically mapped visual and somatosensory cortices, but for which the second dimension besides time is space, as this is the topographically mapped feature in these modalities (as opposed to tone frequency in the auditory system). Indirect evidence for this comes from a study [170] showing that while contralateral somatosensory inputs reset ongoing oscillations to their high excitability phase, ipsilateral inputs reset them to their low excitability phases in auditory cortex. In the visual domain, studies showing opposing changes of perceptual sensitivity in distinct locations during spatial attention tasks also hint at the existence of spatiotemporal phase map entrainment by either saccades and microsaccades, or the fixation-related visual input [10,171,172].

To summarize, there is plenty of evidence that entrainment establishes at least two-dimensional, but possibly multi-dimensional, ‘phase-maps’ within sensory cortical regions that essentially model relevant properties of sensory objects and thereby enhance their sensory representation compared to the background (‘local effects’ of phase specific entrainment). The mechanism for ‘background attenuation’ is two-fold: sensory inputs that occur in synchrony with attended ones but do not match the attended features will be suppressed by the low excitability phases aligned to their timing (for example, suppressing the ‘orchestra’ when listening to a particular instrument in a musical piece), while sensory inputs ‘out of synchrony’ with attended ones will be attenuated compared to attended ones by receiving the ‘random phase treatment’ (suppressing chatter in the audience). That is, while attended inputs always arrive at high excitability phases of entrained oscillations, out-of-synch inputs will arrive at random phases of the entrained oscillation, thus their sensory representation will be weaker and unstable (for example, unattended speakers during a cocktail party).

possible evidence for ‘parsing by entrainment’ in the pulvinar and A1 [36], but further experiments will be required to verify this notion. Besides parsing the sensory input stream, entrained oscillations might also be responsible for the parsing of internal information, thereby forming the backbone of the neuronal syntax in the brain [184].

Caveats

Last but not least, we must also include a cautionary note on entrainment functions. Just because the effect of entrainment or in general rhythmic activity is observable in behavioral performance or electrophysiological measures, it does not mean that it contributes to the specific task the individual or their brain is performing. For functionality to be claimed, it has to be shown that entrainment either meaningfully modulates some other variable — for example, ERPs or firing of an ‘attentional spotlight neuronal ensemble’ — or results in a behavioral benefit, and even so, like everything described in this section, the hints for functionality remain correlational. Ultimately, the selective knock-out of entrainment via pharmacological or viral methods will provide us with answers on the precise nature of entrainment functions, but until then, we feel it is useful to form firm theories that can be tested by future neuromodulation experiments. This brings us to our last section, where we imagine what brain operations would be like if oscillatory entrainment did not exist.

A World without Entrainment

Based on the entrainment functions outlined above, if neuronal oscillations could not be aligned to the temporal structure of relevant input streams, at a minimum this would result in unstable processing of sensory inputs, and thus unstable sensory representations. This could present as impaired intensity perception, which was described in both the auditory and visual modalities in schizophrenia patients [185–187]. The reason this is worth mentioning here is that it has been demonstrated that schizophrenia patients fail to exhibit oscillatory entrainment by attended rhythmic auditory streams [188], which correlates with their behavioral deficits and clinical symptoms. Therefore, in this section we will envision how perceptual and cognitive processes would be altered in a brain without neuronal entrainment, and try to link the imagined effects to symptoms observed in neuropsychiatric and developmental disorders.

If we imagine how primary auditory cortex would operate without phase-specific entrainment when presented with a stream of tones, there are two possible scenarios. In both, excitability would randomly fluctuate in relation to the timing of the tones. In the best-case scenario, this excitability would be synchronized across A1 neuronal ensembles tuned to process different frequencies. In this case, while inputs related to the pure tones would be randomly modulated, resulting in the above described unstable intensity perception, at least frequency tuning would be stable due to matching phases across neighboring neuronal ensembles. In the worst-case scenario, excitability would fluctuate randomly across neighboring neuronal ensembles, resulting in a random bias in tone frequency perception. This is because if, for instance, region 1 is in its high and region 2 is in its low excitability phase, inputs arriving to both regions simultaneously will be amplified in region 1 relative to inputs arriving in region 2, and the sum will be a frequency bias towards whatever frequency region 1 is tuned to. Such a scenario could underlie congenital amusia (aka tone

deafness [189]), and would also explain why schizophrenia patients require much larger frequency differences than controls to be able to differentiate pure tones [188,190].

A lack of orchestrating coherent oscillatory dynamics across different modalities would result in impaired multisensory processing, specifically the impairment of temporal integration, which is one of the main sensory deficits in autism spectrum disorders, hypothesized to underlie the language and communication deficits that are key symptoms [191]. In fact, a lack of entrainment would also hinder interpersonal synchronization, which is a key aspect of communication among a wide variety of species including humans [73,78,192–194].

The lack of sensory-motor coordination established by oscillations entrained across sensory and motor regions [35,70] would at a minimum manifest as impaired synchronization of motor actions to sensory stimuli, and likely overall arrhythmic motor patterns. An impairment of tapping ‘in-phase’ with auditory stimuli was observed in both schizophrenic patients [195] and in developmental dyslexia [196,197]: in both groups, the precision of tapping synchronization to auditory stimuli, or tapping rhythmically in general, is reduced.

Impaired sensory-motor coordination could also lead to reading impairments, which provides another potential link to developmental dyslexia. Recent studies indeed indicate that rhythmic entrainment at timescales relevant to speech (syllabic rate) are disrupted in dyslexia [198,199]. If entrainment is responsible for parsing sensory and internal information, the lack of entrainment would result in impaired speech learning and perception, thus it might be the underlying deficit.

Moreover, if top-down entrained oscillations form the basis for parsing and transmitting information not related to sensory inputs — for example, self-referential thinking or memory recall — the effects of not being able to coordinate oscillatory activity for these ubiquitous mechanisms would result in wide ranging cognitive deficits.

It is up for future studies to determine whether the sensory-cognitive impairments listed in this section that could theoretically be explained by the lack of entrainment are indeed causal, which we think is a worthwhile endeavor since if it turns out that at least some of them are, we might be able to devise stimulation strategies to rectify or at least amplify entrainment and thereby restore its functionality.

Finally, we would also like to point out that while there is substantial emerging evidence for the importance of entrainment in brain operations, this does not mean entrainment is a one-size-fits-all solution. For instance, besides entrainment, there are certainly other types of predictive timing mechanisms in the brain [72], but we do not see these as competing, rather as complementary in those cases when a rhythmic temporal structure is lacking.

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