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Title: Oscillations in the auditory system and their possible role

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Highlights

- Interpretation of auditory oscillations in confused by methodological issues
- Neural entrainment and oscillations likely have distinct mechanisms
- Gamma oscillations seem solidly established in the auditory cortex
- The role of oscillations in primary and non-primary auditory areas may differ
- Rhythmic inputs remain crucial for auditory processing

Abstract

GOUREVITCH, B., C. Martin, O. Postal and J.J. Eggermont. Oscillations in the auditory system and their possible role. NEUROSCI BIOBEHAV REV XXX XXX-XXX, 2020. - Neural oscillations are thought to have various roles in brain processing such as attention modulation, neuronal communication, motor coordination, memory consolidation,

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decision-making, or feature binding. The role of oscillations in the auditory system is less clear, especially due to the large discrepancy between human and animal studies.

Here we describe many methodological issues that confound the results of oscillation studies in the auditory field. Moreover, we discuss the relationship between neural entrainment and oscillations that remains unclear. Finally, we aim to identify which kind of oscillations could be specific or salient to the auditory areas and their processing.

We suggest that the role of oscillations might dramatically differ between the primary auditory cortex and the more associative auditory areas. Despite the moderate presence of intrinsic low frequency oscillations in the primary auditory cortex, rhythmic components in the input seem crucial for auditory processing. This allows the phase entrainment between the oscillatory phase and rhythmic input, which is an integral part of stimulus selection within the auditory system.

Keywords: Auditory cortex; oscillations; local field potential; EEG; rhythmic neural activity; entrainment

1. Introduction

In the first report of EEG in humans, H. Berger (1929) tried to characterize and block fundamental rhythms of the brain occurring around 10Hz. Since then, various roles for neural oscillations have been suggested, such as: feature binding, memory access, information transfer, and central pattern generators related to motor output. Oscillations are also linked to cognitive states such as sleep, awareness and consciousness. While the role of oscillations has long been widely investigated and heavily discussed in olfactory (Kay et al., 2009), visual (Eckhorn et al., 1988) and somatosensory systems (Nicolelis et

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al., 2001), this role appears more debated in the auditory system and in the auditory cortex in particular. What is then specific to the auditory cortex?

In the first parts of this review, we quickly summarize the context in which the different frequency band activities are observed in the auditory cortex. We then argue that many scientific, methodological and computational biases may have so far contributed to confuse the interpretation of oscillations and suggest that the word “oscillation” should be used with more caution, particularly in the auditory field. In particular, the precise localization of many oscillations observed in human studies is distinctly unclear. Moreover, oscillations as currently used in papers sometimes involve many broadband and/or transient activations and many processes relating to neural entrainment, all with little discussion.

Finally, we examine whether there is a specificity of the neural code in the auditory system. Sensory systems differ in the particular properties of the physical signals that they encode. Sounds, which are an essential communication vector in many species, contain very fast temporal and frequency modulations, which carry a great deal of information. In this real-time auditory processing, which involves short time-constants and fast neural recovery up to at least the primary auditory cortex, the role of fixed frequency oscillations appears unclear. Moreover, as we ascend the hierarchical pathways of the auditory system, the involvement and importance of slow oscillations (classically: Alpha, Theta, Delta, Tau) relative to faster oscillations could progressively increase as the information tends to be gradually recoded and modulated, and the timescale for auditory information processing lengthens. In the last section of this review, we try to decipher the presence of oscillatory networks in A1 and auditory associative areas with regards to their anatomical and functional difference and their perceptive roles. Although addressing all types of oscillations appears as a difficult challenge, we do think that such a big picture is necessary to reconsider their role in auditory processing.

Overall, we argue that the presence of oscillations, and specifically low frequency oscillations, in the auditory system could be less frequent than expected from the

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literature, particularly in A1. We examine this hypothesis and endeavor to identify which kinds of oscillations could possibly be specific or salient to the auditory areas and their processing.

2. Rhythmic EEG in the auditory cortex

Principles of oscillation generation, classification of frequency bands and description of their respective roles can be found in the appendix A, B of this review or in other papers (Wang, 2010; Ward, 2003). As a general principle, lower frequency oscillations propagate better in brain tissues, which are natural low-pass filters (Hindriks et al., 2016), suggesting a role in coordinating very distant areas (Kopell et al., 2000). Indeed, it is noticeable that mostly low frequency oscillations (1-10 Hz) such as alpha waves appear during both ongoing activity and inactivity and are therefore associated with mental states such as relaxation, concentration, or attention. On the contrary, faster oscillations (>10 Hz), such as beta and gamma, are often related to stimulus or motor processing. We only seek to refresh here some of the main observations and questions raised regarding oscillations in the auditory cortex.

2.1. High-frequency band activity (Gamma, 30-200Hz)

Overall, the presence of gamma-band activity in the Local Field Potential (LFP) of the auditory cortex seems solidly established in both animals and humans. In animals, both spontaneous and induced gamma activity has been observed. For instance, in halothane-anesthetized rats, gamma (around 50Hz) oscillations in bursts of 4-5 periods were found both spontaneously and after electrical stimulation of the thalamic posterior-intralaminar nuclei (Barth and MacDonald, 1996; Sukov and Barth, 1998). Also, using awake cats, Vianney-Rodrigues et al. (2011) observed that passive listening to tone-pip stimulation induced short-latency bursts of gamma activity in A1 in the low-gamma (30–70 Hz) and high-gamma (90–150 Hz) bands at long (up to 350 ms) and variable latencies. Interestingly, such gamma oscillations were only locally coherent with spiking activity.

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Gamma band activity also appeared during an associative memory task in the rat (Headley and Weinberger, 2011). Following a classical fear-conditioning task associating a tone (CS+) and a shock, the subsequent discrimination between the CS+ stimulus and an unconditioned one elicited long-lasting broadband gamma activity in A1. Throughout the duration of the training, this gamma activity increasingly correlated with the spiking activity related to the CS+ stimulus (Headley and Weinberger, 2013). Interestingly, the strength of gamma oscillations paralleled learning and was predictive of the acquisition of the associative memory as well as the receptive field plasticity observed for the CS+ stimulus (Headley and Weinberger, 2011). In another recent study, fear discrimination in rats elicited an increased coherence in the low-gamma range (40-70Hz) between A1 and prelimbic areas that was predictive of the behavioral choice (Concina et al., 2018).

In contrast with the animal research, in humans, where evoked gamma was first identified by Pantev et al. (1991), auditory-stimulus-induced broad-band gamma oscillations mainly occur at higher frequencies of around 80 Hz (Billig et al., 2019; Ross et al., 2020). Further, they generally occur as a predominantly transient response to stimulus transitions (Edwards et al., 2005; Griffiths et al., 2010; Sedley et al., 2012).

The mechanisms for gamma generation have long been studied and would rely on very generic principles involving either pyramidal-interneuron or interneuron networks (Tiesinga and Sejnowski, 2009; Whittington et al., 2000). In-vitro studies showed that anatomical networks of the primary auditory cortex (A1) are compatible with the generation of gamma (Ainsworth et al., 2011). Gamma oscillations are typically strongly modulated by acetylcholine, whose muscarinic M2 and nicotinic $\alpha_4\beta_2$ receptors are abundant in the auditory cortex as in many sensory areas (Zilles and Palomero-Gallagher, 2017).

2.2. Mid-frequency band activity (Beta, 10-30 Hz; Alpha, 8-15Hz; Spindle waves, 7-14Hz)

Mid-frequency band activity in awake animals is likely the least common in the auditory cortex, especially in small animals. For instance, beta oscillations are rarely observed in

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the auditory cortex itself, even after conditioning. This is especially true in rodents: training rats in an olfactory-auditory task elicited a beta oscillation for which the olfactory bulb, the piriform cortex and the perirhinal cortex were found coherent, but which was weakly observed (Olofsson et al., 2019) or remained absent in the auditory cortex (Gnaedinger et al., 2019). However, broad beta-band activity is modulated in many cerebral areas associated with auditory perception in human and non-human primates (see e.g. (Arnal et al., 2015; Bartolo and Merchant, 2015; Breska and Deouell, 2016; Fujioka et al., 2012)). Indeed, an interval of beta event-related desynchronization, i.e. a decrease of beta-band activity, has been shown as an obligatory response to sound almost across the whole spatial extent of MEG recordings (Mazaheri and Picton, 2005).

As in other cerebral areas, the presence of alpha band activity during the ongoing activity, which was observed in A1 in the awake macaque (Haegens et al., 2015), could be related to vigilance states (Nir et al., 2015). Indeed, there is a negative relationship between ongoing alpha rhythm and neuronal firing in A1 (Haegens et al., 2015) (as in V1 and S1) but no relationship between passive stimulation (pure tones) and alpha power. The evidence for the intrinsic existence of alpha rhythms in the auditory cortical fields is sometimes made difficult by its frequency band overlapping with the more classical theta and delta bands. For instance, alpha activity is replaced by delta and theta activity in spontaneous LFP in the macaque Lakatos et al. (2005). Also, throughout the 1990s, a large number of studies, mainly in human magnetoencephalography (MEG), observed a specific rhythm around 10Hz in the auditory areas, which was assigned “tau” rather than alpha. Still, this rhythm has similarities with classical alpha features since it appears during spontaneous activity rather than evoked activity, and is affected by auditory input (Lehtelä et al., 1997; Niedermeyer, 1991). It also disappears during auditory memory scanning tasks (Kaufman et al., 1992; Rojas et al., 2000).

In addition to these classical frequency-band related activities, sleep spindle oscillations are widely reported as “bursts” of oscillations lasting 1-3 seconds in the band 7-14Hz, and are typically observed during barbiturate anesthesia or in the natural sleep early stages

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and slow-wave active phases. They could be a correlate of memory formation (Gais et al., 2000) and synaptic plasticity (Steriade and Timofeev, 2003). Similar to sleep, spindle oscillations synchronize over large cortical areas, including auditory areas. The source of spindles seems to stem from the thalamus and more precisely the interaction between thalamic reticular neurons and thalamocortical cells (Steriade et al., 1985; Steriade and Deschenes, 1984; von Krosigk et al., 1993). However, ketamine-induced spindles in the cat A1 have stimulus-dependent properties that resemble those of the alpha rhythms, particularly that they are suppressed by sound (Britvina and Eggermont, 2008a), which questions the validity of the 'blockade of synaptic transmission' in the thalamus proposed by Steriade and Llinas (1988). Suppression could in fact occur through activity of the specific auditory pathway (Britvina and Eggermont, 2008b) or, alternatively, via the brainstem reticular formation bypassing the thalamus and activating higher-order auditory cortex, which in turn modulates A1.

2.3. Low-frequency activity (Theta, 4-10Hz; Delta, 1.5-4Hz)

While low-frequency activity in the auditory cortex has been described in guinea pigs (Farley and Noreña, 2013) and rats (Cambiaghi et al., 2016), it has mostly been investigated in human and non-human primates.

There are several papers from the lab of Lakatos showing theta as well as delta (around 1.4Hz) and gamma oscillations in spontaneous or tone-evoked laminar LFP recordings in macaque's A1, both in absence (Lakatos et al., 2005) or in presence (Lakatos et al., 2007) of a simultaneous somatosensory stimulation (Fig. 1D). According to the first study above, delta (1–4 Hz) phase modulates theta (4–10 Hz) amplitude, and theta phase modulates gamma (30–50 Hz) amplitude, similar to hippocampus (Buzsáki et al., 2003) and entorhinal cortex (Chrobak and Buzsáki, 1998). Canolty et al. (2006) also found that gamma band activity was often locked to theta phase in A1. Theta phase would therefore be more important than the amplitude for cross-frequency coupling. This is also in agreement with the study by Ng et al. (2013) in humans and macaques, which found that stimuli which can be discriminated by firing rates can also be discriminated by phase

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patterns related to theta's band but not by oscillation amplitude. In terms of information coding, advantages of such a phase-based code are numerous: not only could theta phase serve as a common frame of reference between information locally available at individual neurons and complementary information spread over a mesoscopic scale, but the phase of such slow cortical rhythms could also help in reducing the effects of sensory noise (Kayser et al., 2009). Consistently, delta oscillations would act to gate influences of temporal expectation on perception (Herrmann et al., 2016).

Very slow rhythms (<1Hz) are most often filtered out in LFP recordings and thus they are rarely mentioned or emphasized. However, to the best of our knowledge, no mention of such very slow oscillations has been reported in the auditory cortex. UP and DOWN states, which are subthreshold two-state behavior of the membrane potential of neurons silencing and favoring action potentials generation, respectively (Steriade et al., 1993b), have been sometimes assimilated to slow-wave oscillations (Destexhe et al., 2007; Mahon et al., 2006; Steriade et al., 1993b, 2001). However, this remains controversial: Wilson (2008) argued that UP and DOWN states, which are typically arrhythmic, result from ionic conductance changes far from the oscillation generators, and that tissue slices where UP and DOWN states are observed are free from slow-wave oscillations. In any case, network properties make these large-amplitude slow "oscillations" visible in LFP and voltage-sensitive dye imaging signals in the auditory cortex (Farley and Noreña, 2013).

3. Methodological issues with the interpretation of oscillations in the auditory system

When interpreting the oscillations described above and looking for mechanisms, one must be aware of several biases, some of them particularly exacerbated in the auditory field.

3.1. Localization of oscillation generators remain unclear

The above imbalance between human and animal studies involving mid-frequency and low-frequency band activities might also reveal that neural oscillations could be

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associated to more complex processing involving associative areas and top-down modulations. Indeed, behavioral paradigms are kept simple in animal models, especially for rodents, and non-primary sensory areas are also typically less studied (and anatomically less well defined). We will come back later on the relationship between top-down modulation and oscillations (section 5.2) but we suggest here that the unclear localization of oscillation generators is confusing their role in auditory processing.

In humans, although there has been considerable progress in recent decades, source localization techniques applied to scalp MEG/EEG data (i.e. the inverse problem) are still not trustworthy at the millimeter scale. This is necessary to distinguish A1/BA41 (in the Heschl Gyrus) from AII/BA42 (at the border of the gyrus) for instance. Even the ECoG techniques have no access to the deeply buried Heschl Gyrus that contains A1 in humans. As a matter of fact, delta, theta and even alpha/tau and beta band activity were observed in various MEG/EEG/ECoG studies but neural correlates can never be localized more precisely than in “auditory regions” (Abbasi and Gross, 2019; Arnal et al., 2015; A. Chang et al., 2016; Doelling et al., 2014; Doelling and Poeppel, 2015; Gross et al., 2013; Herbst and Obleser, 2019; Lehtelä et al., 1997; Leske et al., 2014; Müller et al., 2013; Park et al., 2015; Pefkou et al., 2017; Teng et al., 2018).

In fact, when precise localization of recordings can be assessed through intracerebral implantations, oscillations other than broadband gamma are much more likely to appear in non-primary areas (Morillon et al., 2012). For instance, in humans during navigation tasks, some theta oscillations were noticed in the temporal lobe (Kahana et al., 1999), possibly at the location of auditory belt. In animals, gamma oscillation bursts were found in an area “overlapping the boundary of primary and secondary auditory cortex” (Barth and MacDonald, 1996), possibly serving to synchronize interactions between the primary (A1) and secondary (A2) areas (Franowicz and Barth, 1995). Even if this is an indirect argument, it is likely that a massive presence of oscillations in A1 would have been easily noticed given the many teams having recorded in animal’s A1 for decades. The comparatively few studies outside of A1 suggest a more likely source.

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These observations suggest that many high-level processes, whose oscillations are neural correlates, could in fact relate to non-primary/associative auditory areas. After all, even the generators of the early N1/N100 wave are known to be already outside of A1 (Godey et al., 2001; Liégeois-Chauvel et al., 1994). This does not mean that oscillations are not involved in auditory processing but that they might be more important after a certain extent of neural recoding. The information available at the A1 stage would still be in a "crude" language to higher-order cerebral areas involved in cognitive networks. This view is consistent with the fact that responses tend to be less stimulus-driven and oscillations more induced as we get farther from A1 (Morillon et al., 2012). As suggested by these authors, these code transformations occurring between the auditory core and belt, and then from belt to parabelt, could possibly correlate with sustained spiking modes, compatible with rate coding principles (Singer, 1999). Still, such ideas remain hypothetical. The code transformations and therefore the different use of oscillations could also build on anatomical differences. The cytoarchitectonics of primary and associative auditory areas are very different (Morosan et al., 2001) and it is likely that this is also true for the capillary networks (Harrison et al., 2002). Further, with regards to the densities of receptors across sensory areas, A1 is very close to the primary somatosensory cortex, but again, core and belt auditory areas notably differ (Zilles and Palomero-Gallagher, 2017). Perhaps more importantly, cortical connections within the auditory cortex were found to be very hierarchical: contrary to other primary sensory areas, A1 is connected almost exclusively with the narrow surrounding belt of cortex and very little with more distant associative auditory fields, which therefore have little access to the auditory core information (Kaas and Hackett, 2000). This would contribute to partitioning the auditory neural code into clearly separated levels of cortical processing (core, belt, parabelt).

Overall, a more precise localization of oscillation generators is clearly a necessity to reconcile animal and human data to better understand the neural recoding of the sensory information, which is a current challenge in neuroscience. The use of large animals with

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well-defined auditory cortical areas and complex behavioural skills, from the ferret to the non-human primate, might be the only sound model to achieve that program.

3.2. The ambiguity of phasic responses: evoked potentials or phase resetting?

Another confusing element in the interpretation of oscillations holds in the very nature of the LFP/EEG signal used to observe them, which represents the neuronal activity only indirectly through the – possibly distant - flow of the extracellular currents of both excitatory and inhibitory neurons (Bédard et al., 2004; Buzsáki et al., 2012; Einevoll et al., 2013; Teleńczuk et al., 2017). Within these compound signals, responses to the onset of an acoustic event in subcortical and cortical auditory pathways typically elicit what is called an auditory evoked potential (AEP). The role of AEPs could be to detect acoustic edges and transients (Fishbach et al., 2001) and more generally to enhance surprising or new events among auditory streams. While those events are single and stereotyped, their spectral content has energy in specific bands that could possibly be confused with oscillations (Fig. 1), a concern already raised in (Ray and Maunsell, 2011). Such effects of band-pass filtering of AEPs, possibly exacerbated by non-causal filtering, can be seen for instance in Fig. 2A-C in (Vianney-Rodrigues et al., 2011) or Fig. 2A in (Noda et al., 2017). The difference between AEPs can also easily generate spectrally and temporally focused energy as shown in Fig. 1Aii. In fact, when the phase-locked part of auditory events or task related responses is isolated, it tends to match the spectro-temporal pattern generated in this manner (see e.g. Fig. 4 of (El Karoui et al., 2015) or Fig. 5 in (Morillon et al., 2012)). This simplistic concern should not be underrated: the Fourier decomposition of a signal is a mathematical property, not a biological one. The specific temporal shape of a waveform does not inform how it was created in neural networks.

(Insert Fig. 1 about here)

Nevertheless, there have been two main alternative theories trying to reconcile AEPs with oscillations. First, it has been intriguingly observed that the AEP component around 40Hz was correlated (at the individual level) with the ability of the auditory cortex to phase lock to 40Hz stimulations (Zaehle et al., 2010). The authors interpret this as a resonance

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frequency of the auditory cortex circuits that could in fact be a unified theory accounting for the stereotyped AEP shape seen in an impulse response, the specific 40Hz steady state response and also the solid presence of gamma oscillations in the auditory cortex. Such resonance frequencies are in fact characteristic time constants of the brain that could account for some perceptive abilities such as gap detection (Baltus and Herrmann, 2015) or even intelligibility in general (Baltus and Herrmann, 2016).

A second and old theory for AEP generation (Sayers and Beagley, 1974), more recently revived for visual evoked potentials (Jansen and Brandt, 1991; Makeig et al., 2002), suggests that AEPs could be based on the synchronization of the EEG-rhythm generators. The idea of Sayers and Beagley (1974) was that stimulation with clicks or tone pips could also synchronize the largely random rhythmic activity of groups of neurons and make it visible at the scalp. In other words, the AEP would be the result of the sudden phase resetting of all rhythmic ongoing activities present in the neural signal. This idea is not that easy to prove, even mathematically. Simulations showed that the interpretation of ERPs as evoked potentials or phase-resetting might depend on the weak or high levels, respectively, of ongoing and stimulus-related activity (David et al., 2005). However, AEPs typically contain very strong onsets and therefore sharp edges (Vianney-Rodrigues et al., 2011), possibly more than in any other cerebral area due to the conjunction of the strength of thalamo-cortical inputs to A1 and their precise timing governed by the interplay between excitation and inhibition (Wehr and Zador, 2003). These sharp edges in LFP/CSD often induce spurious co-modulation between the phase or signal of low frequency activity and the high frequency activity (Kramer et al., 2008). Sharp edges could therefore yield overestimated co-modulations and phase resetting found in the auditory system. In fact, Mäkinnen et al. (2005) examined single-trial auditory MEG data in humans and found that auditory stimuli do not give rise to phase reorganization of ongoing activity. Further, the relationship between spectral power and the amplitude of event-related responses can be accounted for by a linear summation of the event-related response and ongoing oscillation with a stochastically distributed phase. They concluded that auditory event-related responses are unique descriptors of neural information

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processing in humans, generated by processes separated from and additive to ongoing brain activity. However, the debate does not seem completely closed at present (see also section 4.5).

3.3. Short or broadband oscillations are ambiguous

In many studies, careful examination of spectrograms reveals ultra-short "oscillations" whose status may therefore appear ambiguous. The duration is sometimes only one cycle for delta, two cycles for theta and roughly four cycles for gamma oscillations (see e.g. Fig. 6 in (Lakatos et al., 2007) reproduced in Fig. 1D here, Fig. 2 in (Arnal et al., 2015), Fig. 1 in (Arnal and Kleinschmidt, 2017)). In these cases, as stated before, it is difficult to disentangle neural oscillations from the spectral content of typical evoked potentials. For instance, AEPs or inter-trial phase locking lasting only one or two cycles were possibly misinterpreted as "alpha-beta" activity (Fritz et al., 2010) or "theta" activity (Musacchia et al., 2017; Zhang et al., 2016). More importantly, it questions the accuracy of the conclusions based on very few cycles of oscillations.

Another long-term debate concerns the status of broadband oscillations. The beta-band activity modulated in many cerebral areas in auditory perception, in both human and non-human primates, is often broadband (see e.g. (Bartolo and Merchant, 2015; Breska and Deouell, 2016; Fujioka et al., 2012)). Further, gamma band activity described in animals (Headley and Weinberger, 2013, 2011) and humans (Billig et al., 2019; Edwards et al., 2005; Griffiths et al., 2010; Morillon et al., 2012; Ross et al., 2020) is broadband. Narrowband gamma oscillations, which are common in the visual system (see e.g. (Hoogenboom et al., 2006)), and are the result of oscillations in the retina (Castelo-Branco et al., 1998), have not been identified in the auditory domain (Sedley and Cunningham, 2013). This is important because narrowband and broadband oscillations might originate from different mechanisms and therefore serve distinct roles. Narrowband gamma, at least in the visual system, would act as an inhibitory process (Sedley and Cunningham, 2013) while broadband activity would be heavily influenced by the phase of low-frequency band activity and would thus be a reliable predictor of neuronal spiking, even

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in the auditory cortex (Fries et al., 2001; Mukamel et al., 2005; Pesaran et al., 2002; Rasch et al., 2008; Whittingstall and Logothetis, 2009). In fact, it was suggested (Chen et al., 2007; Cruikshank et al., 2002; Juergens et al., 1999; Kaur et al., 2004; Kreiman et al., 2006; Miller, 2010; Miller et al., 2009, 2007; Milstein et al., 2009; Mitzdorf, 1985) and then shown (Manning et al., 2009) that widely described correlations between spikes and gamma-band LFP activity are actually due to broadband LFP patterns, rather than band-specific oscillations. In the most extreme case, strong correlation between high-frequency gamma oscillations with multi-unit spiking activity could simply reflect spectral leakage from multi-unit activity (Jacobs et al., 2010; Ray and Maunsell, 2011).

We suggest at least two ways to better understand broadband activations, especially in the gamma range. First, spiking activity should be analysed simultaneously to the LFP activity or, if not possible as in humans, sampling rate should be chosen above 500Hz. As already pointed by (Jacobs et al., 2010), a sampling rate limited to 200-300Hz will prevent the experimenter to observe the power at frequencies higher than 100-150Hz and lead him to inaccurately describe the signal as being limited to the ~70–150-Hz "high gamma" band. Second, it is possible that broadband activations result from the grand average of narrowband activations with varying central frequencies across trials. One future challenge is therefore to design analyses that detect oscillations *in the single trial*. In some sensory systems that are very oscillatory by nature, for instance the olfactory system (Laurent, 2002), the observation of single trials leaves no doubt about the presence of oscillations and whether they are induced or evoked, see Fig. 2.

(Insert Fig. 2 about here)

3.4. Spectral processing of EEG activity can create artificial oscillations

Brain activity in any structure, when recorded by extracellular microelectrodes or large scalp electrodes over very long periods, has a spectrum that approaches a 1/f shape the longer the recording occurs. This spectral shape is known as "pink noise" in physics (Miller et al., 2009). Such remarkable invariance of the neural activity across location and scale (Freeman et al., 2000; Milstein et al., 2009), in addition to a minimal stability required by

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brain dynamics, has been demonstrated to lead to a power law for temporal fluctuations (Bak et al., 1987). This theoretical explanation, which mainly considers the brain signal as a noise with a self-similar fractal structure, has been questioned by some authors who argue that brain patterns observed on short time windows show a narrower spectrum and therefore can actually be considered as mostly oscillatory (Buzsáki and Watson, 2012). This is implicitly the point of view of some authors from the auditory field that assimilate the narrowband-filtered EEG activity to neuronal oscillations (Giraud et al., 2007). This view is defendable but, as already stated above, the Fourier components of a signal do not ensure that these components biologically exist (Fig. 3). Moreover, there is a clear risk of finding artificial oscillations by clustering them as in Fig. 4. As stated previously, detecting significant oscillations in the single trial and observing their consistency in central frequency or duration would lead to more solid conclusions.

(Insert Fig. 3 about here)

(Insert Fig. 4 about here)

3.5. Comparison with other sensory systems is still incomplete

Another future challenge in rhythms understanding is to have a more global view of cortical activity. Most studies target one area or two and, given the differences in species, electrodes and protocols, ongoing and evoked activity is still hardly comparable across studies. Moreover, when recording more global networks, there are inconsistent results regarding the importance and prominence of intrinsic cortical rhythms in the human auditory cortex compared to other cerebral areas. Groppe et al. (2013) objectively characterized the types of electrocorticography (EcoG) oscillations commonly observed when an individual is awake and immobile with eyes closed. Their results support the importance and prominence of theta oscillations in general cortical function, including superior temporal areas where the auditory cortex is located. Using MEG, Mellem et al. (2017) found predominance of intrinsic delta (but less theta) band activity in the auditory cortical activity of humans as well as a peak in high gamma (>100Hz possibly correlated to multiunit activity as previously shown). Delta and gamma band activity were strong in

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the auditory cortex compared to other areas. Another MEG study rather found predominance of alpha+theta (Keitel and Gross, 2016). Studies trying to elucidate large-scale networks by the joint analysis of electroencephalography (EEG) and functional magnetic resonance imaging (fMRI), found predominance of delta+theta activity in the auditory processing networks (Liu et al., 2014; Mantini et al., 2007). Inconsistency of results calls for further investigations. Additionally, these studies mostly examined resting states where involvement of cortical networks can be compared between cerebral areas. Consistency with entrainment studies, which rather emphasized the importance of delta/theta+gamma activity in the human auditory cortex (see section 4.2, 4.3) is not completely clear yet. It is true that comparing event-related responses in distinct sensory systems is very difficult and rarely done (Olofsson et al., 2008). Optogenetics could provide a technical possibility as it unifies the protocols with no regards to the physical properties of sensory stimuli. The level of similarity between sensory and optogenetic network activation will need further investigation to this purpose, but it is starting to be explored (Schmid et al., 2016).

4. Entrainment of neural activity: is there a relationship with oscillations?

4.1. Entrainment is ubiquitous in the auditory system

Neural entrainment occurs when the spectrum of the neural activity is able to mimic specific temporal fluctuations of the sensory stimulus. As stated in section 3.1, neural entrainment is particularly studied in the auditory system and has been less clear in the visual system (Capilla et al., 2011) and even more so in other sensory systems. According to Zoefel and VanRullen (2017), this is because a rhythmic component in the input is crucial for the auditory, but not the visual system.

In humans, there has been a wide literature reporting entrainment of auditory cortical activity in both delta/theta and gamma frequency bands (Gross et al., 2013). For instance, the spectrum of stereo-electroencephalographic signals in response to speech was correlated with the envelope fluctuations of speech mostly within theta and gamma

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frequency bands in A1 and the auditory associative area Brodmann 22 (Fig. 5, Giraud and Poeppel, 2012). Some authors suggest that entrainment at specific frequencies would actually be endogenous cortical rhythms in A1, providing temporal and spatial constraints on the neuronal mechanisms underlying auditory cortex processing: indeed, in fMRI experiments coupled with single units or EEG recordings in humans, it was found that spontaneous (Giraud et al., 2007) and evoked (Mukamel et al., 2005) EEG power variations correlated with the A1 cortical synaptic activity, especially in the theta band (right A1) and gamma band (left A1). In addition, in macaques, O'Connell et al. (2015) observed that for delta and gamma stimulation rates, the amplitude spectrum of neuronal activity is ''peaked'' compared to the spontaneous spectrum one would expect from steady-state response. However, lower amplitudes around the peak in the related spectra of the auditory stimulus stream result in no significant net amplitude change in the delta and gamma bands. The authors suggest that the peaks could therefore represent a reorganization of oscillatory activity to match relevant temporal scales, which would be characteristic of oscillatory entrainment (Haegens and Zion Golumbic, 2018). However, there have been recent critics on experiments trying to match the frequency spectrum of the stimulus to the EEG spectrum (frequency-tagging approach). Indeed, in the case of beat perception, the stimulus envelope spectrum can be rendered identical while perception is different (Henry et al., 2017; Rajendran and Schnupp, 2019).

4.2. Low-frequency entrainment

Auditory entrainment has been reported for essentially all frequencies between 0.5 and 10 Hz (Ding and Simon, 2014; Gross et al., 2013; Ng et al., 2013) but it is under current debate if the entrainment stems from the same mechanisms for all frequencies (Ding and Simon, 2013; Kayser et al., 2015; Park et al., 2015). In fact, there is no current evidence that the neural entrainment even relies on the same mechanisms as, and is similarly segmented as, classical delta/theta/alpha bands. Therefore, we suggest avoiding these latter names to describe neural entrainment as it might bias the interpretation. The current consensus is that core and belt auditory areas are able to phase-lock with slow

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temporal fluctuations below 10-15Hz (Giraud et al., 2000; Gourévitch et al., 2008; Joris et al., 2004; Liégeois-Chauvel et al., 2004) which likely contributes to this specific cortical sensitivity. Consistently, it was recently shown in the bat that phase coherence of spikes and LFPs in the theta–alpha range (4–12 Hz) was strongest for neurons that are able to track the periodicity of the stimulus in a phasic manner (García-Rosales et al., 2018).

As an interpretation of neural entrainment, the alignment between oscillatory phase and rhythmic input (phase entrainment) would be an integral part of stimulus selection in the auditory system and a fundamental feature of the auditory system (Haegens and Zion Golumbic, 2018; Zoefel and VanRullen, 2017). It likely has evolved due to the rhythmic nature of the auditory environment. Indeed, the entrainment in the 1-10Hz band remarkably corresponds to speech envelope, i.e. regularities arising from syllabic rate and phonemes (Ahissar et al., 2001; Aiken and Picton, 2008; Keitel et al., 2017; Luo and Poeppel, 2007; Park et al., 2015). Those fluctuations also correspond to those present in voice and musical instrument periodicity, speech prosody, and musical rhythms (Ding et al., 2017, 2016). These interpretations found in human studies apply little to animal acoustic environments. Therefore, it is critical to increase investigation of low-frequency entrainment in animals, especially rodents. As a more generic principle, the way the acoustic signal is processed by the peripheral auditory system, one temporal envelope exists for each cochlear channel so that entrainment on the global temporal envelope could also subserve interchannel spectral integration in all mammals.

4.3. High-frequency entrainment

In the gamma band, the entrainment has long been emphasized in “40Hz” human EEG/MEG studies: steady-state responses to auditory stimuli are enhanced in EEG and MEG at stimulation frequencies around 40Hz (Galambos et al., 1981; Mäkelä and Hari, 1987). The mechanisms of this are not completely clear. As stated previously (section 3.3), some authors argue that the increase in the specific 40Hz could be interpreted as a sequence of ERPs (Bohórquez and Özdamar, 2008) or alternatively build on the resonance frequencies of specific GABAergic populations and mechanisms, similar to the induction

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of gamma band response generation (Lewis et al., 2005; Ross et al., 2005; Vohs et al., 2010). Sources are not clear either: the phase-locking around 40Hz could be of subcortical origin and then involve the interaction of cortical networks mainly within the temporal and frontal lobes (Farahani et al., 2017; Reyes et al., 2005; Tang et al., 2016). Interestingly, the 40Hz auditory steady-state response is also observed in rats (Kozono et al., 2019), suggesting that a hardwired circuit configuration in the thalamocortical system might be shared between mammals. Further investigation in mammals is required though.

4.4. Is neural entrainment a passive or active mechanism?

The auditory system is considered to be very fast when compared to other sensory systems: transduction latencies are much shorter for vestibular and auditory stimuli compared to tactile stimuli and especially for visual stimuli. This contributes, in part, to shorter reaction times for sounds than for lights, touches or head movements (Barnett-Cowan and Harris, 2009) or shorter latencies in event-related potentials (Olofsson et al., 2008). The consequence of short time constants in the auditory system is also the fast recovery of neural adaptation: at the scale of a few dozens of milliseconds, the absence or presence of an acoustic signal is accompanied by the absence or presence of a neural response, respectively. Thus, there clearly is a passive component in auditory-related neural entrainment. Does such passive entrainment also involve more active processing? This is crucial to decipher its functional role and whether it has one (Rimmele et al., 2018).

Obleser et al. (2012) provide a strong argument about speech entraining theta oscillations in auditory cortex: slow brain oscillations become phase-locked to slow spectral regularities in an auditory signal, even in the absence of amplitude envelope fluctuations. More recently, there have been attempts to separate the entrainment trivially due to the "passive following" of rhythmic changes in sound amplitude and spectral content from that possibly elicited by a more active tracking of higher-level cues. Zoefel and Van Rullen (2017; 2015) proposed to construct a speech/noise hybrid stimulus with spectral content comparable across phases of the original signal envelope so that only "high-level" cues (mostly phonetic information) remain temporally fluctuated. In monkey A1, such stimuli

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still elicited neural entrainment to speech signals. While the construction is mathematically relevant and clever, it is clear that some spectrotemporal structure remains in those artificial speech signals (see Fig. 2 in (Zoefel and VanRullen, 2015)). Therefore, the argument of the authors that such stimuli might not "passively entrain the lowest levels of auditory processing such as the cochlear level, where speech and noise would excite the same cells to the same extent" remains to be proved. The auditory nerve and the immediate subsequent neural nuclei have been proved to very efficiently extract fine spectrotemporal cues and it is still unclear how, and at which stage, the inter-channel processing occurs to integrate and identify harmonic or spectrally structured signals from noise.

4.5. Can we talk about "oscillations"?

Entrainment at a given frequency sounds like a resonance frequency of some intrinsic oscillating networks, which "filter" and track the time course of a stimulus parameter such as amplitude modulation. Even if the term "brain oscillations" is often used in the context of entrainment, what is important here is essentially an arrhythmic phase locking to temporal fluctuations and not an induced rhythmic oscillation. In other words, the oscillation cycle rate directly depends on the cyclic rate of the stimulus parameter. Additionally, one major difference between induced rhythmic oscillations and entrainment is the lack of, or weakness in, resonance in the entrainment. That is the short duration of damping with entrainment mostly vanishes after the stimulation ends. This means that entrainment can be particularly short, even to just a few cycles (see e.g. Fig. 4a in (Giraud and Poeppel, 2012)). Those two properties of entrainment raised questions about how to disentangle the contribution of evoked responses to entrainment as a specific neural process (Lenc et al., 2018; Novembre and Iannetti, 2018; O'Connell et al., 2015). Moreover, the phase distortion induced by event related potentials might bias or even mislead the interpretation of entrainment (Zoefel and Heil, 2013).

Recently, there has been an attempt to explicitly distinguish between oscillations and a sequence of evoked responses (Doelling et al., 2019). The idea is that in an oscillatory

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model, where the frequency of the oscillation matches that of a repetitive stimulus, the cosine function corresponding to this oscillator appears in the EEG with a mostly stable phase, irrespective of the stimulation rate. However, in an evoked model, because the response is modeled as a convolution of the stimulation envelope and a typical response kernel, an increase in the stimulation rate should have little influence on the time lag and therefore randomize the phase between the peak EEG and the stimulation. The authors show that for various stimulation rates of musical notes, the MEG/EEG response in the temporal lobe is more accurately predicted using an oscillator model than an evoked one. The idea is clever and should be pursued, but some issues still remain: the method assumes that the evoked auditory response is a short peak present in each cycle. As illustrated in the Fig. 6, this is questionable. The evoked response in A1 to a smooth stimulus, such as amplitude modulated noise, can range from: an onset peak, to a temporal response mimicking the stimulus envelope, to a combination of both within the same cerebral area, and even from one cycle to another. Neural adaptation or habituation, predictive timing, top-down modulations and feed-forward suppression can strongly modulate not only the onset but possibly the steady-state portion as well. Overall, the nonlinear transform from the original temporal envelope to the evoked response challenges the central hypothesis of the evoked model that the time lag between the peak stimulus and the peak response is constant with the stimulus presentation rhythm.

To some extent, there are similar difficulties raised in classical animal studies using spectrotemporal receptive fields to predict the temporal response to complex sounds. 20-50% of this response can be explained by the reaction to simple sounds, but nonlinearities stemming from adaptation and complex spectrotemporal integration of the neural response cannot be fully reproduced (Laudanski et al., 2012; Shechter and Depireux, 2010; Thorson et al., 2015; Williamson et al., 2016). In other words, the evoked response is not necessarily a typical kernel and its variations can strongly modulate the phase or time lag computations.

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Does this mean the oscillatory model is absent? Probably not, but this is a good example where the absence of precise spatial localization of recordings (as in most human studies, see section 3.2) confuses the interpretation of putative oscillations. The EEG/MEG is already a grand average of neural signals originating from many auditory areas which may differ in their neural code, the presence of onsets, of top-down modulations and, in the end, of oscillatory activity.

(Insert Fig. 6 about here)

5. Are oscillations important in the auditory system?

Summing up the evidence and the issues related to oscillations that we described in previous sections, we could state as a simplified model, the following: that A1 mostly involves high-frequency evoked oscillations in the gamma band and neural entrainment in the low-frequency range, while as we go higher in the hierarchy of auditory associative areas, information would be coded in a mode increasingly compatible with inducing or processing oscillations. We examine here possible roles for oscillations in the auditory cortex.

5.1. Communication across brain regions

Neuronal oscillations within and across brain regions have been proposed as playing a crucial role in the communication between brain regions. Gamma has long been hypothesized to play a role in communication within the auditory cortex, such as between core and belt/parabelt areas (Franowicz and Barth, 1995; Potes et al., 2014). At a larger scale, Bonnefond et al. (2017) discuss a theory in which communication between two regions is established by phase synchronization of oscillations at lower frequencies (< 25 Hz), which serve as a temporal reference frame for information carried by high-frequency activity (> 40 Hz). This framework, based on hierarchical nesting of frequencies, posits that cross-frequency interactions are essential for understanding how large-scale cognitive and perceptual networks operate. There is evidence for such a frequency–space trade-off in the brain (Buzsáki et al., 2012; Steriade, 2006). In the auditory cortex, it has

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been hypothesized that theta rhythms, which coincide with the syllabic rate, could track speech as well as orchestrate gamma neural activity that is possibly involved in coding phonemic details (Canolty et al., 2007; Ghitza, 2011; Giraud and Poeppel, 2012; Pefkou et al., 2017). Multi-scale sensory analysis of speech has been shown to be theoretically credible and efficient by neural microcircuit models (Hyafil et al., 2015). Alternatively, gamma could be nested on neural entrainment. In any case, these theories currently lack experimental evidence in both humans and animals. In particular, it remains unclear how and whether such multi-scale analysis of speech would propagate bottom-up from A1 or belt/parabelt areas to higher-order cognitive areas. Top-down aspects of auditory processing, which we now examine specifically, have been explored in more detail.

5.2. Top-down modulation

There are at least two possible roles for top-down modulation of the auditory cortex. The first one would rely on extracting supra-segmental components from complex sounds such as speech and the second one would be to optimize neural processing through prediction of future events.

First, extracting supra-segmental speech components such as intonation, prosody, and irregular speech rate requires longer time scales, compatible with rhythms in the delta range. Further, as was hypothesized by Fries (2005), in order for conduction delays between areas to avoid interfering with oscillations, they should be an order of magnitude shorter than the cycle length of the oscillation. For these reasons, and because passive listening and complex auditory tasks elicit delta band activity in the EEG (Arnal and Kleinschmidt, 2017; Molinaro and Lizarazu, 2018), it has been hypothesized that delta entrainment could be a candidate for top-down control of auditory cortex, at least in humans, reflecting higher-order speech processing mechanisms such as syntactic structuring of the input (Ding et al., 2016; Meyer et al., 2017). Conversely, the alterations of such top-down modulations could subserve pathologies such as dyslexia (Molinaro et al., 2016).

As a general model, low-frequency entrainment could be generated (and stronger) in

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associative rather than in primary auditory cortices (Giraud and Poeppel, 2012) and could possibly be driven by (Kayser et al., 2015; Park et al., 2015) or modulate (Keitel et al., 2017) activity in fronto-parietal networks. For instance, there is a rich literature on how the motor cortex modulates the auditory cortex during speech perception (review in (Morillon et al., 2019)). In short, it is hypothesized that motor delta-beta phase amplitude coupled oscillations would optimize the parsing, encoding and processing of slow linguistic information.

When previous information is available, the brain is also trying to optimize the processing of any future event. This is because the brain has only one trial to process in natural acoustic environments. A second role of top-down modulation would be to predict a stimulus, which relies on at least two main questions: what happens - predictive coding - and when - predictive timing - (Arnal and Giraud, 2012; Noda et al., 2017). Predictive coding impacts post-stimulation responses and is sometimes shown as a modulation of auditory evoked responses such as N1/P2 (Costa-Faidella et al., 2011; Zhang et al., 2009). There has been a recent and increasing trend to consider both delta and particularly beta band activity as involved in top-down predictive coding (Abbasi and Gross, 2019; A. Chang et al., 2016; Chang et al., 2018; Herbst and Obleser, 2019; Iversen et al., 2009), with late post-stimulation activations (latencies > 100ms). However, the localization of oscillation generators remains unclear and most studies show very transient and weak modification of the neural signal (one or two cycles at best of a putative oscillation). This questions whether the description of specific frequency band activations is appropriate in this context.

Anticipating the temporal occurrence of an upcoming event improves the quality of auditory information and therefore the behavioural decision: this is called predictive timing (Morillon et al., 2019). The main hypothesis states that the phases of neural oscillations would temporally modulate the pre-stimulus excitability of task-relevant neural populations in the sensory cortical areas as well as fronto-parietal areas (Morillon et al., 2019; Noda et al., 2017; Rimmele et al., 2018). Alpha reduction and phase angles in

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the alpha band are the main candidates currently identified to impact prediction and to correlate with attention (Cao et al., 2017; Lakatos et al., 2016; Strauß et al., 2015; Wilsch et al., 2015). The pre-stimulus modulation is extremely short in duration (200-400ms), which means there are very few cycles at this frequency range. In fact, in the literature of anticipation, predictive temporal cues considerably amplify a potential link to anticipation and motor preparation, a phenomenon known for decades as the contingent negative variation (CNV, Nobre and van Ede, 2018; Walter et al., 1964). It remains to be proven whether alpha reduction relies on similar or different mechanisms than CNV. In any case, the pre-stimulation cue is one slow wave and one could consider it more a timely modified excitability than an oscillation strictly speaking ((Breska and Deouell, 2016) and see Fig. 1 in (Arnal and Giraud, 2012)). The slowness is crucial here: in predictive timing or in neural entrainment, the baseline drift visible before the expected, or the next stimulus, respectively, provides a context for its processing (Breska and Deouell, 2016; Lakatos et al., 2008; Schroeder and Lakatos, 2009; Zhou et al., 2016) with tolerance for some temporal jitter.

Note that at the level of A1, the gamma activity would be involved in both extraction of acoustic components and prediction error and would rather propagate bottom-up (Arnal and Giraud, 2012; Cao et al., 2017) but would be top-down modulated by delta-beta activity from auditory associative areas (Fontolan et al., 2014). This latter study uses simultaneous intracerebral recording in primary, non-primary and higher-order cognitive areas with precise localization, which seems the only reliable methodology to achieve solid conclusions in top-down modulation studies. Further, there is clearly a strong overemphasis on speech, which is specific to humans, in studies dealing with top-down modulations and communication between areas in general. Filling the gaps between animals and humans would require using more natural auditory scenes (excluding speech), if we hypothesize that many acoustic components seen as salient and then detected, identified, and recoded by the auditory cortex of both human and animals are similar.

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Beyond top-down modulation, there is in our opinion, one intriguing point: that the auditory system is remarkably robust to exogenous oscillations. Nasal respiration related fluctuations generated in the olfactory system synchronizes local field potential activity in other brain regions such as amygdala and hippocampus (Zelano et al., 2016) but also primary somatosensory cortex and primary visual cortex, possibly to modulate local gamma activity (Rojas-Líbano et al., 2018; Tort et al., 2018). Critically, we have not found any report of respiration-entrained oscillations occurring in the auditory cortex.

Also, auditory areas remain active in NREM sleep, likely because of their important role as a warning detector, and acoustic stimulation often suppresses sleep-related slow rhythms (Issa and Wang, 2013; Sela et al., 2016). Most authors working on sleep indicated that A1 activity was remarkably preserved during NREM (Edeline et al., 2001; Issa and Wang, 2008; Peña et al., 1999; Sela et al., 2016) and even during spindling (Britvina and Eggermont, 2008b). Slow wave sleep induces changes in receptive fields (Edeline et al., 2001) as well as a reduction in the detection of quiet sounds and sound-evoked response suppression (Issa and Wang, 2011), suggesting a modification of the excitation-inhibition interplay during sleep. Nevertheless, whether or not this robustness of auditory processing to exogenous oscillations is related to a different role of oscillations in auditory cortices remains to be determined.

5.3. Relationship with perception

The role of oscillations in auditory perception remains unsettled. At the brain scale, it has been hypothesized that binding several objects and emotions into a single experience could depend on rhythmic synchronous firing (Singer, 2007), possibly including nested frequencies (Bonnefond et al., 2017; Palva and Palva, 2018), which is hypothesized to allow for fast and robust communication across distributed networks. As we saw previously, the phase of neural oscillations – alpha in particular – prior to stimulation could influence or predict both the subsequent neuronal response and the stimulus perception. This is shown in many sensory-motor systems and extensively in the visual system (Busch et al., 2009; Foxe et al., 1998; Haegens et al., 2012, 2011; Händel et al.,

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2011; Mathewson et al., 2009; Meeuwissen et al., 2011; Payne et al., 2013; Thut et al., 2006). However, the evidence is less strong in the auditory cortex in humans. In fact, what evidence there is that complex auditory perception tasks, memory tests, and decision-making lead to induced or modulated neural oscillations, particularly in humans and in the alpha and theta bands, is shown outside of the auditory cortex (Dimitrijevic et al., 2017; Pesonen et al., 2006; Recasens et al., 2018; Walz et al., 2015; Yu et al., 2017).

Additionally, while learning is known to modulate, or increase, the power of oscillations in other sensory systems (Brickwedde et al., 2019; Martin and Ravel, 2014; Zold and Hussain Shuler, 2015), evidence of such modulations is still controversial in the auditory system. Learning related modulations of gamma activity in rodents were observed during classical conditioning by some authors (Headley and Weinberger, 2013, 2011) and not by some others (Jeschke et al., 2008). The effects of low frequency oscillations have rarely been investigated. One study has reported that in the secondary auditory cortex of rats, theta band activity could modulate the activity of the basolateral amygdala in the recall of remote fear memories (Cambiaghi et al., 2016). An indirect link between oscillations and perception has been emphasized : auditory illusions (such as those elicited by Zwicker Tones) would be accompanied by a decrease in alpha power, even in the primary auditory cortex (see e.g. a review in (Lange et al., 2014)). However, it must be noted that almost none of the studies have been replicated.

In fact, beyond the auditory cortex, it is still debated to what extent oscillations may play a functional role for brain processing, as opposed to being a mere epiphenomenon, i.e. simply correlative markers of micro-neuronal fluctuations. This long and vehement controversy, particularly for gamma band (Cardin, 2016; Fields, 2018; Fröhlich and McCormick, 2010; Ray and Maunsell, 2015; Sohal, 2016) could only be solved by showing causal relationships between oscillations and perception, i.e. how perception is affected by the manipulation of oscillations independently of other cerebral processes, such as spikes. This theoretical purpose has remained unreachable to date, but volitional control of oscillations (Engelhard et al., 2013; Fetz, 2013) and non-invasive brain stimulation

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techniques (Andoh et al., 2018; Heimrath et al., 2016; Neuling et al., 2012; Zoefel and Davis, 2017), even if mechanisms for this latter remain controversial (Karabanov et al., 2019; Liu et al., 2018), are promising attempts. For instance, the use of transcranial alternating current stimulation (tACS, Herrmann et al., 2013) at 40Hz in the auditory cortex selectively modulated speech perception (Rufener et al., 2016b), in an age dependent fashion (Rufener et al., 2016a). A 4Hz modulation also improved click detection thresholds in silence for certain phase relationships between modulation and stimulation (Riecke et al., 2015a) and improved detection of sounds drowned in noise (Riecke et al., 2015b). In future, the use of tACS, which is a completely silent procedure contrary to transcranial magnetic stimulation and which targets a specific frequency contrary to transcranial direct current stimulation, to either synchronize or desynchronize neural oscillations, could reveal more direct evidence of the role of oscillations in perception, even in non-specialized auditory areas (Albouy et al., 2017). Also, as we previously saw, predictive timing, which shows that the phase of oscillations could temporally modulate behavioral performance, provides results in favor of a role for oscillations in the auditory cortex.

5.4 Parsing the information

While perception is commonly regarded as a continuous process, another old theory states that oscillations could actually divide the continuous sequence of inputs into a series of discrete perceptual cycles (VanRullen and Koch, 2003). The parsing function of neuronal oscillators would also determine the length of an information unit (Buzsáki, 2010; Buzsáki and Watson, 2012). This hypothesis received experimental support based mostly on alpha oscillations in the visual system (Jensen et al., 2014) and in the somatosensory domain (Baumgarten et al., 2015) However, in the auditory system, these discrete perception cycles do not appear to be present (Zoefel and Heil, 2013). VanRullen et al. (2014) argued that this does not necessarily mean that auditory perception proceeds continuously. Instead, they propose that audition could still involve perceptual cycles, but auditory cycles may need to sample the input stream more flexibly, by adapting to the temporal structure of the auditory inputs. Indeed, the risk of using regular oscillations in

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the auditory system is a “blind” subsampling of the sound environment that might destroy its temporal structure. This hypothesis of flexible parsing would be consistent with the three levels of parsing currently described in the auditory cortex: first, the gamma band activity generated in A1 or belt areas could subserve a first temporal integration window around 20-25ms, building on the natural resonance of cortical networks in A1 and on neural encoding time scales (Ince et al., 2013). Second, in belt areas, and possibly in A1, and beyond the neural entrainment, temporal fluctuations in the theta range (~100ms) could reflect an encoding or parsing of acoustic features, for instance to segment speech, or more generally, to “chunk” acoustic streams (Doelling et al., 2014; Ghitza and Greenberg, 2009; Hyafil et al., 2015; Kayser et al., 2015; Teng et al., 2018). Indeed, theta entrainment and speech intelligibility are similarly affected by adding background noise or noise-vocoding to the speech signal (Ding et al., 2014; Ding and Simon, 2013; Peelle et al., 2013). Third, the delta entrainment would more likely reflect perceived qualities of speech, such as irregular speech rate, and would provide top-down control over auditory cortex as we saw previously. Of note is that the hypothesis regarding theta and delta currently is restricted to human auditory processing since we showed that low-frequency band activity is rarely studied and observed in non-primate animals (section 3.1).

This flexible parsing would be necessary in the auditory system, where there is a high probability to encounter new “surprises” or events in the fast changing acoustic signal. These events, such as a modification of the short voice-onset time in speech processing, or occurrences of clicks in rhythms in music, may completely change the phonemic, semantic and prosodic content of the complex sound. The retinal persistence, which mechanically limits the processing rate of the visual system to a 10^{th} or a 15^{th} of a second, is between one and two orders of magnitude larger than the auditory system. These unanticipated events constrain the auditory system to “reinitialize” the auditory network quickly and frequently as well as to perform predictions on longer time scales. Thus, we could suggest that what matters more for the auditory cortex is the ability to modulate excitability as a function of context (stream, masking, and syllable/vocalization) rather than predictable oscillations.

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5.5. Subcortical pathways hardly show oscillations

Excepting UP and DOWN states in the auditory (non-lemniscal) thalamus (Gao et al., 2009; He, 2003), there has been, to the best of our knowledge, no study showing oscillations (other than auditory steady-state response) in the MGB and the inferior colliculus. However, the IC might include neurons with intrinsic regular spiking similar to chopper units (Rees et al., 1997). The geometry of such nuclei is organized circularly, rather than in columns as in the neocortex, which makes the summation of dendritic potentials quite small and therefore makes the LFP unpredictable. Still, this absence of oscillations is in contrast with subcortical nuclei from the visual system (Bal et al., 2000; Foik et al., 2018; Le et al., 2019).

At the thalamic level, it has been hypothesized that the parsing of sensory information into “packets” may help to coordinate activity across neuronal groups that are also in subcortical regions (Haegens et al., 2015). For instance, the recurrent thalamo-cortical resonance might organize a temporal binding of sensory information into a perceptive whole (Bollimunta et al., 2011; Llinas, 2002). However, this has mostly been observed in the visual system (Hughes et al., 2004) and during different stages of sleep (Llinás et al., 1998; Steriade, 1997; Tsai et al., 2010, p. 201) but not in the auditory system except maybe during thalamocortical dysrhythmia (Moazami-Goudarzi et al., 2010).

Another source of subcortical oscillations could stem from the periphery: cortical oscillators in various species and non-auditory modalities exhibit frequency ranges that match their corresponding sensory channels (Ahissar and Zacksenhouse, 2001). The alpha and gamma frequent oscillations in the visual cortex could match those of retinal activation frequencies (Castelo-Branco et al., 1998) caused by miniature eye movements (Ahissar and Arieli, 2012). There is also a possible match between oscillations around 30Hz found in the tactile afferent units and in the somatosensory cortex in the monkey (Ahissar and Vaadia, 1990; Johansson et al., 1982). Contrasting with this, there is no known shared intrinsic rhythm at any particular frequency associated with hair cells, except in the bullfrog vestibular system (Ramunno-Johnson et al., 2009).

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6. Concluding remarks

Let us now try to summarize the main points. There is no doubt that neural oscillations in the human auditory cortex are more frequently observed than in smaller animals: in particular, beta, tau, alpha and theta rhythms are notably absent from most rodent studies (see Appendix C). Therefore it is not completely surprising, but remains remarkable that recent reviews about auditory cortex processing in animals tend to make little or no mention of oscillations (Blackwell and Geffen, 2017; King et al., 2018; King and Nelken, 2009; Nelken et al., 2014; Wang, 2018). One could argue that the more complex auditory tasks considered by humans such as speech processing, contributes to this discrepancy. However, this discrepancy also exists in the visual system. More likely, global EEG/MEG recordings dilute the localization of cerebral areas but allow complex cognitive processes to be accounted for. Conversely, the role of cerebral networks is less understood in animals but the recordings are better localized. Further investigation of behavior coupled with simultaneous electrophysiology in large animals is clearly required (note that the limited temporal resolution of 2-photon imaging discards its use for direct oscillation studies). Moreover, the complex relationship between spiking activity and local field potential during oscillations is only discernable in animals due to the invasive techniques required.

The precise localization of recordings in animals helps to better understand the roles of the distinct areas within the auditory cortex. This precision is rare and difficult to achieve in humans and in fact the auditory cortex is often seen only as a whole in many human studies. We argue that the primary auditory cortex may have a specific neural code, which is of little compatibility with the wide and efficient use of low-frequency oscillations found in other neural areas. Indeed, generators of intrinsic oscillations in larger animal A1, as reflected in the resting state LFP spectrum, appear limited to gamma, which possibly builds on intrinsic properties of local cortical inhibitory networks. Also, the general view is that alpha rhythms are linked to inhibitory control, with low levels of alpha reflecting a state of excitation, whereas high levels of alpha indicate a state of inhibition

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(Klimesch et al., 2007). Since the auditory cortex is constantly "listening" and monitoring our environment even under sleep or anesthesia, alpha levels would then be generally low especially in A1 (Billig et al., 2019; Weisz et al., 2011 but see Haegens et al., 2015 for opposite results). After A1, there could be a progressive recoding of the auditory information that would gradually involve more oscillations as we go from more to less auditory-specialized areas and from specific representations of auditory objects to feature binding (see Fig. 7). This hierarchical partitioning of the neural code might be specific to the auditory cortex. Indeed, topographic organization or complex feature selectivity for instance, are not as widely distributed between primary and non-primary areas, when compared to somatosensory, olfactory and visual systems (Casagrande and Kaas, 1994; Johnson et al., 2000; Krubitzer and Kaas, 1990). Moreover, in contrast to the primary visual and somatosensory systems, discrete perceptual cycles, resulting from intrinsic alpha and low beta-band (8–20 Hz) modulations of the input are not present in the auditory system. Such deep integration within the somatosensory, olfactory and visual areas might favor oscillations as a communication vector. One challenge in future research is to clearly understand how auditory areas communicate with each other, with higher-order auditory areas or even other sensory ones.

(Insert Fig. 7 about here)

We acknowledge that rhythmic components in the input are likely crucial for auditory processing (Zoefel and VanRullen, 2017), allowing phase entrainment between oscillatory phase and rhythmic input as an integral part of stimulus selection in the auditory system. In particular, theta entrainment would mainly reflect perceptual processing of the auditory signal while delta entrainment would involve additional higher-order computations in the service of language processing. Many aspects of the functional and perceptive roles for neural entrainment remain unclear though. It is tempting to establish a parallel between the great flexibility in the network dynamics required by such entrainment and the very broad modulation of oscillatory bands that are shown generally

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across human auditory studies. In contrast with the olfactory system, there is little to no evidence for very narrowband oscillations throughout the auditory system.

The many studies showing very short and broadband gamma band activities give rise to doubts on the existence of true oscillations as we saw that they largely overlap with spectral contributions of auditory evoked potentials or spiking activity. We suggest here that authors become much more circumspect regarding the use of the term oscillations, especially in human studies. As long as the mechanisms behind population neural signals such as the EEG/MEG (and therefore the AEP) are not completely understood, it will remain intricate to accurately interpret waveform shape modifications in the Fourier space. Moreover, neural entrainment should be clearly distinguished from oscillations because its mechanisms likely differ.

Among the various types of oscillations observed in the central nervous system, the presence of gamma band activity in the primary auditory cortex appears to be the best established in both humans and animals. Its functional role remains unclear in the auditory cortex (as it is in many other cerebral areas): gamma oscillations can appear from relatively simple stimuli and do not seem to be modulated by learning. They might actually be involved in surprise responses (prediction violations) and more generally in comparison to target sounds (Jeschke et al., 2008; Sedley et al., 2016). Further investigation is needed on eliciting gamma band activity as a function of behavioral output.

The above points should not be seen as negative or controversial. We observe that the number of studies showing low frequency oscillations in the auditory cortex are in contrast with the importance given to oscillations in EEG studies in neuroscience and that attention should be drawn to this. Moreover, we saw that the particular focus on oscillations might be biased by methodological considerations insofar as mostly EEG/MEG is available in humans. We hope that this review will at least raise newer fruitful queries about the specificity of oscillations in the auditory neural code.

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Appendix

A. What is an oscillation? From theory to observations

EEG recordings can be classified in to three distinct groups (Logothetis, 2002): rhythmic, arrhythmic and dysrhythmic. The first two, i.e. oscillations, and no stable rhythms, appear in normal subjects and refer to waves of approximately constant frequency content. The last refers to pathological rhythms in patient groups and will not be examined in this review.

From this classification, neural *oscillations* are rhythmic, or repetitive, neural activity in the central nervous system. They are present from the scale of a single neuron up to mesoscopic (local neuron group) and the macroscopic (brain regions). The common conception is that *evoked* oscillations are phase-locked to a stimulus while *induced* oscillations are not. An induced oscillation appears as an increase of oscillatory activity during a mental process; that is, its phase may differ across measurements. Nevertheless, recent discussions tend to consider those two views as relating to mechanisms closer than previously thought (David et al., 2006). At the single trial scale, an oscillation will provoke an increase in the power spectrum of the EEG spectrogram within a frequency band referred to as an event-related synchronization (ERS). However, the power decrease within a frequency band is called an event-related desynchronization (ERD).

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Oscillations may have theoretical properties of interest for the brain: hypothetically, some randomness could be eliminated by the neural ensemble synchronization process behind oscillations so that they may support information transfer in several ways such as phase-phase coupling, cross-frequency phase-amplitude coupling, or cross-frequency phase-phase coupling (Buzsáki and Wang, 2012; Young and Eggermont, 2009). Oscillations may also improve the efficiency of coding in the presence of synaptic delays (Chalk et al., 2016) and reduce the energetic cost of neural activity by synchronizing the opening of communication windows for input and output (Fries, 2005). Further, phase coding can be used in addition to, or even instead of, rate coding. In other words, the precise timing of excitability changes associated to oscillations allows the consideration of individual spikes rather than firing rates.

Mathematical modeling has shown that the rhythmicity of oscillations may arise from three main dynamic mechanisms: i) harmonic oscillations (small perturbations of a physical system in a minimum-energy state), which were shown to realistically simulate alpha rhythms in the waking EEG as well as slow waves and spindles in the sleep EEG ; ii) limit-cycle oscillators, such as the heartbeat ; iii) delayed-feedback oscillators, which are likely the most widely found neural oscillations. In this latter model, synaptic interactions within a group of neurons may induce synchronization between the neurons and rhythmic changes in their excitability. This occurs through time-delays of synaptic transmission and reciprocal connections forming feedback loops. Synaptic interactions may occur at different spatial scales: local interactions between excitatory and inhibitory interneurons may promote oscillatory activity within a cerebral area (Hoppensteadt and Izhikevich, 1996; Whittington et al., 2000), as described e.g. by the Wilson-Cowan model (Wilson and Cowan, 1973, 1972). Further, long-range feedback loops between brain areas may give rise to oscillations. While various synaptic delays in delayed-feedback oscillators could theoretically lead to oscillations of any frequency, the frequency range of observed neural oscillations does not appear to be random. Therefore, rhythmic EEG can be further subdivided into specific log-scaled frequency bands (Buzsáki and Draguhn, 2004)

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potentially associated to specific cognitive functions: delta (0.5–4 Hz), theta (4–8 Hz), tau/alpha activity (8–12 Hz), beta (13–30 Hz) and gamma (30–200 Hz) (Fig. 8).

(Insert Fig. 8 about here)

B. Oscillations commonly found in cortical areas others than auditory related ones

B.1 Gamma (30-200Hz)

Historically, gamma oscillations have been mostly associated to feature binding (Buzsaki, 2011; Miltner et al., 1999; Singer, 1993). More importantly they are tightly related to perceptual decision mechanisms (Castelhano et al., 2014). Gamma oscillations have been observed throughout the brain: in motor areas as transient bursts, (Cheyne and Ferrari, 2013; Huo et al., 2010), in the hippocampus often coupled with theta (Colgin et al., 2009; Nyhus and Curran, 2010), in prefrontal/frontal areas (Burgess and Ali, 2002), in the olfactory system (Kay et al., 2009) and in the visual system (Jia et al., 2011; Ray and Maunsell, 2011). While oscillations ranging from 30 to 200 Hz can be classified as gamma oscillations, there are different subtypes of gamma likely corresponding to different brain processes, as in the visual system with broadband (30Hz to 160Hz) and narrow-band (40-50Hz) gamma (Bartoli et al., 2019) or in the olfactory bulb (Kay, 2003). Gamma oscillations of the broadband type were also observed in the somatosensory cortex during tactile spatial attention related tasks (Bauer et al., 2006) and in relation to subjective pain intensity (Gross et al., 2007; Zhang et al., 2012). In the hippocampus, very high-frequency gamma-like oscillations (100-200Hz) have been found to be associated with memory consolidation (Colgin, 2016).

B.2 Beta (10-30 Hz)

In general, beta oscillations may emerge from active thinking (such as conditioning) as well as static motor control (Tan et al., 2016). Content-specific beta-synchronization, which act as flexible network dynamics and support the endogenous (re)activation of

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cortical representations, was found during endogenous information processing in working memory and decision-making (Spitzer and Haegens, 2017). Beta is found in the motor cortex during movement execution or planning (Pfurtscheller and Lopes da Silva, 1999; Saleh et al., 2010), in the hippocampus during exploration and associative learning tasks (Berke et al., 2008; Igarashi et al., 2014; Rangel et al., 2015), in the prefrontal cortex in memory and attention-related tasks (Benchenane et al., 2011), in the somatosensory cortex (Ahissar and Vaadia, 1990; Lebedev and Nelson, 1995), and during odor learning in the olfactory system (Martin and Ravel, 2014). Beta is more rarely observed in the visual system, although it is still present (Bekisz and Wróbel, 1993; Schmiedt et al., 2014)

B.3 Alpha (8-15Hz)

Historically, alpha activity was first observed in visual areas during wakeful relaxation with closed eyes. Modulation of alpha power was also found in visual cortex following attentional demands (Worden et al., 2000). Alpha band activity has also been observed in gustatory cortex (Fontanini and Katz, 2005) and in motor cortex (Pfurtscheller and Lopes da Silva, 1999; Saleh et al., 2010). Further, it is possibly modulated by attention, through cerebello-thalamo-cortical loops associated with intermittent motor control (Gross et al., 2002) and has been observed or suppressed in the somatosensory cortex (Ahissar and Zacksenhouse, 2001; Michail et al., 2016). Alpha activity has also been associated with creative thinking in prefrontal areas (Lustenberger et al., 2015).

B.4 Theta (4-10Hz)

Theta oscillations appear strongest in the hippocampus and has been related to navigation, rapid eye movement (REM) sleep, and memory (Buzsáki, 2005; Rutishauser et al., 2010). Theta also appears in active motor behavior (walking, sniffing (Kay, 2005)), in prefrontal areas during complex cognitive tasks (Fuentemilla et al., 2014), is modulated by nociceptive events (P. Chang et al., 2016; Leblanc et al., 2014) and is involved in interactions between the visual system and the short-term memory (Lee et al., 2005; Raghavachari et al., 2006). Theta would also act as nesting oscillations for coordinating

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gamma oscillations during motor planning (Igarashi et al., 2013) and would more generally function as temporal reference (Kayser et al., 2012, 2009; Ng et al., 2013)

B.5 Delta (1.5-4Hz)

Delta rhythms are involved in a great variety of unrelated processes. They have been found to be modulated by movements in the hippocampus in humans (Watrous et al., 2011), Inspiration-locked oscillatory power increases in the delta range were observed in the piriform cortex (Zelano et al., 2016), tied to the timing of the task-relevant cues (Nácher et al., 2013; Saleh et al., 2010), and to the rhythms of visual streams (Lakatos et al., 2008). Delta waves are also typically found during sleep (Steriade et al., 1993c) as well as deep ketamine-xylazine anesthesia (Chauvette et al., 2011).

B.6 Slower rhythms

Slow (< 1 Hz) voltage fluctuations have been observed in EEG recordings (Steriade et al., 1993a). These slow EEG fluctuations are themselves correlated with changes in the power of higher frequency rhythms in the EEG (Buzsáki and Draguhn, 2004), such as in the visual cortex (Leopold et al., 2003) or in attention-demand related networks (Popa et al., 2009). They have been found to be correlated between a number of areas including visual, motor and somatosensory cortices (Chan et al., 2015). In the olfactory system, they could be related to respiration (Fontanini et al., 2003) and they also have been observed in an ultraslow version in hippocampus (Penttonen et al., 1999), even if anesthesia may often influence the presence of such oscillations.

C. The presence of oscillations in the literature

Oscillations are consistently found across species in a remarkable fashion: all known oscillations in humans have also been observed in typical mammals investigated with approximately the same frequency range, notwithstanding some nuances for theta (Aghajan et al., 2017; Buzsáki and Watson, 2012). These preserved characteristics bolster the hypothesis of timing as a strong organizational principle of cortical dynamics. If we adopt a purely quantitative point of view, gamma band appears as the most mentioned

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oscillatory activity in almost all cortices and especially in auditory cortex where it reaches more than 50% of papers studying oscillations. However, quite amazingly, delta, theta and alpha oscillations are also more mentioned in the auditory cortex literature than in other cerebral areas. For such low frequencies, part of the reason lies in the much stronger presence of "neural entrainment" in auditory related publications (Fig. 9A). In particular, almost 70% of publications about delta band activity in the auditory cortex also mention neural entrainment, a percentage three times higher than in the visual system for instance (Fig. 9D). This wide observation of neural entrainment in the auditory system has naturally raised questions about the presence of oscillatory mechanisms but the answer is not necessarily positive and is still under debate in many cases. These debates are examined in section 4.

Also, as a general rule in sensory systems, neural oscillations are typically more often observed in humans (and possibly primates) than in smaller animals. In particular, beta, tau, alpha, theta and even gamma rhythms are notably absent from most animal studies (Fig.9C).

(Insert Fig. 9 about here)

Some technical reasons might bias the studies' outcome: EEG/MEG non-invasive studies, which favor investigations of neural rhythms, comprise the majority of studies in humans, whereas unitary recordings in animals allow deciphering the neural code carried by firing rate, coincident spiking activity and precise spiking patterns. Moreover, oscillations are more difficult to detect in unitary recordings compared to field potentials: periodic excitability changes modulate the probability of firing (and not the firing itself) so that spikes can still be slightly jittered or even missing at the level of an individual neuron and only a sum of neuronal spiking patterns will match all cycles of an oscillation especially for fast oscillations. These purely methodological reasons likely contribute to the same imbalances shown between humans and animals observed in the visual cortex (Fig. 9C).

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Figure 1: Spectral interpretation of evoked potentials particularly in auditory areas can be misleading. Ai) two simulated AEPs (AEP_1: -Γ(3,1/200)+3Γ(4,1/30); AEP_1: -0.8Γ(3,1/150)+5Γ(4,1/30) where Γ(a,b) is the probability density function of gamma distribution with shape (a) and scale (b) parameters) and their time difference. Aii) Waveletograms of the two AEPs and their time difference. Bi) Cortical auditory evoked potential (here in A1 of an anesthetized guinea pig, in response to a click, unpublished data) has narrowband energy in the so-called beta and gamma bands. The AEP was highpass filtered above 3Hz. Bii) Waveletogram of Bi. Note that low frequencies (3-5Hz) are typically dominant in a LFP/AEP. Biii) Bandpass filtered versions of Bi. Causal filtering induces delays, while non-causal filtering is a zero-phase forward and reverse filtering. Bandpass filtered versions of the signal give the impression that oscillations are present

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here. Note the similarity between Biii and Figure 1A in (Noda et al., 2017). C) same as in B with an AEP in response to a sequence of clicks at the rate 6Hz. Note that energy in the gamma band is visible for each AEP while energy at lower frequencies seems more continuous across the whole signal. Also, note that 6Hz rate induces peaks separated by 6Hz, and therefore confusing peaks at 12 and 18Hz (see bandpass filtered versions), according to Fourier decomposition theory. Still, there is no natural oscillation of the neural network here, only an evoked steady-state response. D. Oscillatory properties of auditory responses in the primary auditory cortex of a macaque. Stimulus is a click. Di) Color maps to the left show the laminar profiles of auditory event-related averaged CSD responses for the -500 to 500 ms timeframe. Time-frequency plots to the right show oscillatory amplitudes of the averaged responses for the same timeframe (x axis) with frequency on the logarithmic y axis. Dii) Time-frequency plots show the average oscillatory amplitude of the wavelet-transformed single trials. The traces to the right show the pre-stimulus (blue, -500 to -250 ms) and post-stimulus (red, 0 to 250 ms) amplitudes (x axis) at different frequencies (y axis). From (Lakatos et al., 2007). Note the similarity between Dii and Bii.

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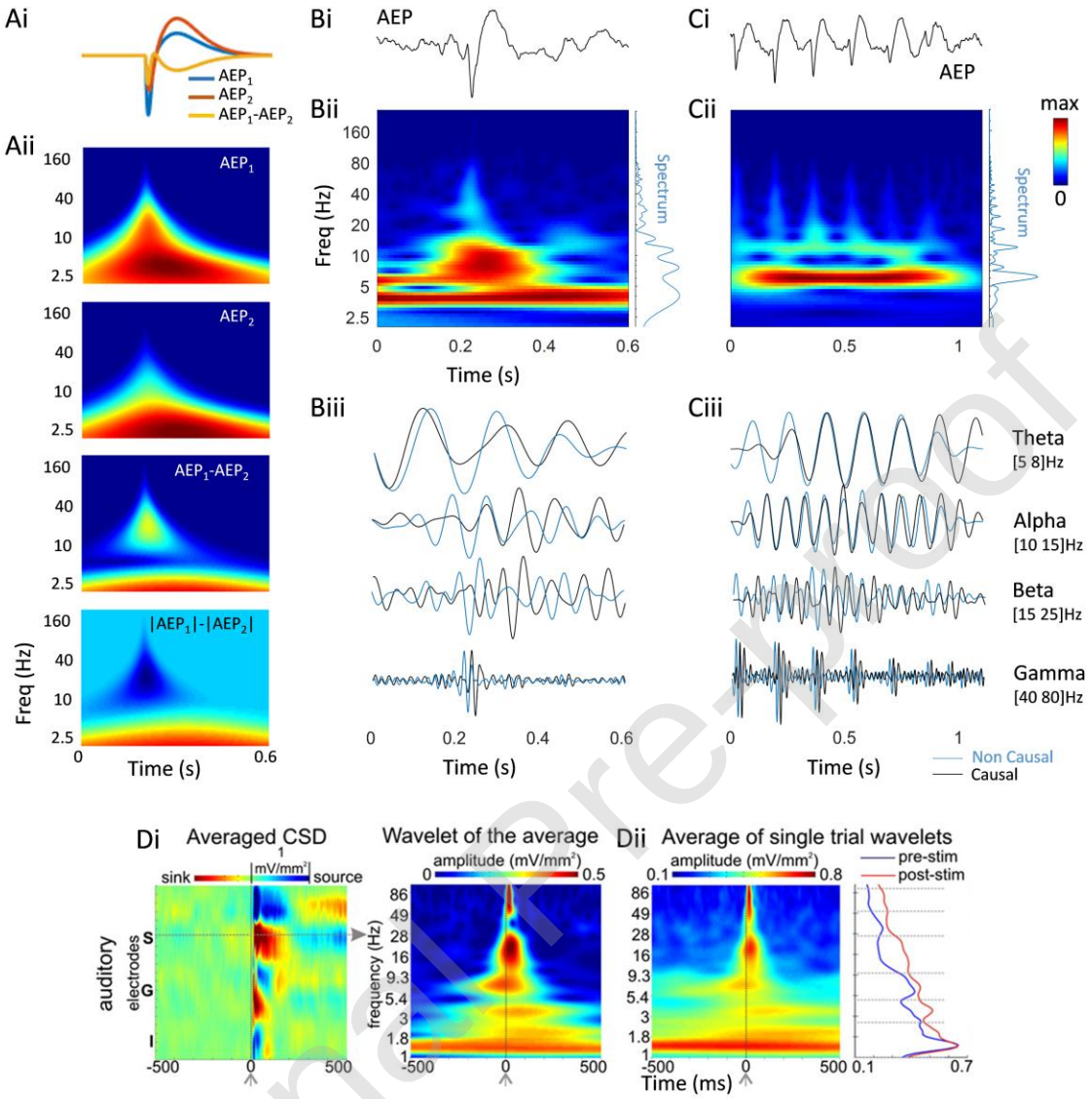


Fig. 2: Olfactory system (here the Piriform Cortex) is strongly oscillatory, especially after conditioning. Theta, beta and gamma bursts are long, frequent and often visible by eye in a single trial. Importantly, they appear as narrowband activations. Top: raw signal; middle: high-pass filtered signal above 10Hz; bottom: waveletogram of the raw signal (same dataset than in (Gnaedinger et al., 2019)).

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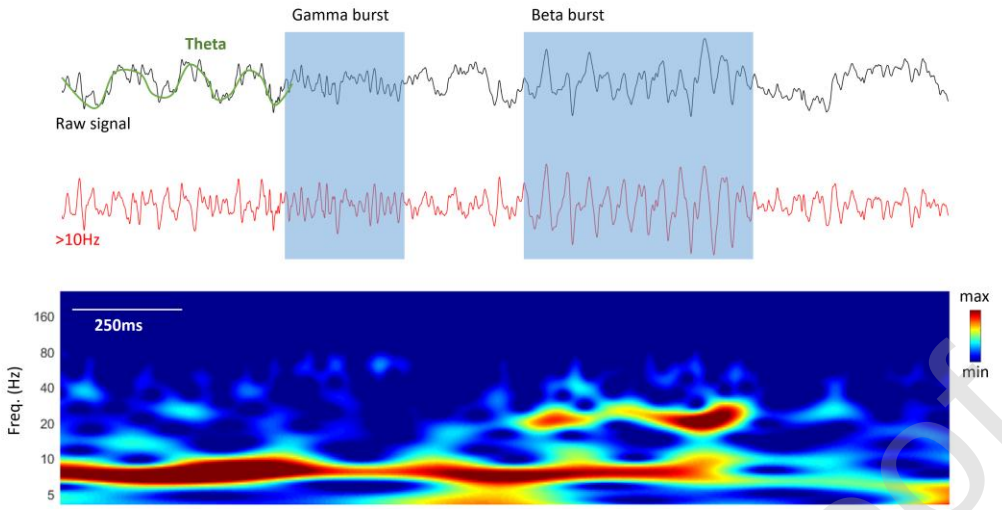


Figure 3: A) Pink noise (close to EEG/LFP typical spectrum) and its bandpass filtered versions in the gamma band (green) and in the very narrowband [50 51]Hz (pink). In shaded blue are excerpts of the signals. B) Frequency spectrum of the long-term (blue) and excerpt (red) of the pink noise. The spectrum computed on a short time scale (0.5-0.6s) shows peaks and therefore seems oscillatory (red), unlike the long-term version over 0-2s (blue). Note that pink noise has an 1/f spectrum which has a linear decreasing energy with frequency in this log scale (dotted black line). C) Spectra of gamma and bandpass filtered versions of the pink noise with colors corresponding to signals in A. Even a narrow-band filtered (random) noise seems oscillatory.

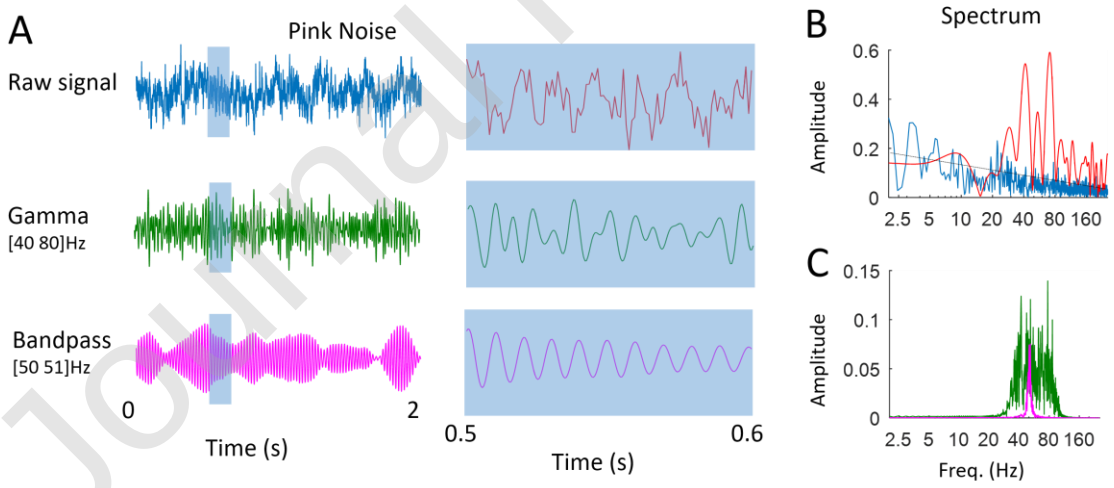


Figure 4: How to find oscillations artificially using a pink noise: first generate a pink noise of 900s (frequency sampling rate 1kHz) and plot its spectrum (A). Cut the signal into 1s segments and normalize their spectrum by dividing them by the average curve in A and subtract 1 to obtain spectra above and below 0 (B). Finally separate the 900 spectrum of segments into 10 clusters using a k-means algorithm (cosine distance) then pick 5 clusters and display their spectrum (C). You might find gamma-peaked and delta-peaked activity. This

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methodology is similar to that in (Keitel and Gross, 2016) and results look similar to the MEG activity reconstructed at rest in the left primary auditory cortex whose Fig. 6a is reproduced here in (D). That does not mean that this type of methodology is inappropriate but rather that the interpretation of short-term components considered as oscillations might be misleading.

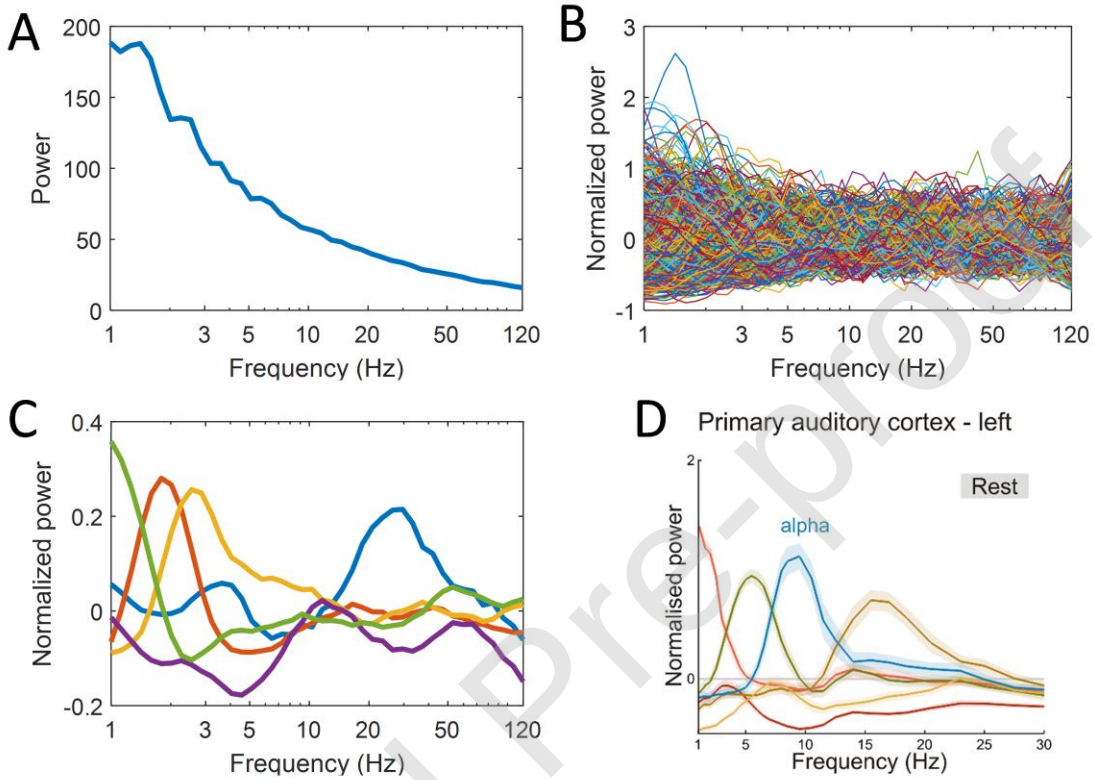


Figure 5: Speech–brain interaction from human intracortical recordings of primary auditory cortex. (A) Time–frequency representation of cortical activity at rest. (B) Time–frequency representations obtained from recordings in A1 made with stereotactic EEG in humans in response to the French spoken sentence “Le nouveau garde la porte.” (C) the same as b in association (Brodmann area 22) cortices (D) Stimulus spectrogram, which shows spectro-temporal modulations and formant structure. (E) An example modulation spectrum extracted from a band centered around 3 kHz (bandwidth 0.5 kHz). To cross-correlate speech with the brain response, the broadband speech spectrum (1–5 kHz) was split into frequency bands (32 channels) from which the temporal envelope in the 1–140 Hz modulation range is extracted. In the band shown, modulations cover this entire range. Auditory cortex power strongly correlates with speech modulations in two frequency bands, theta and gamma. Adapted from (Giraud and Poeppel, 2012).

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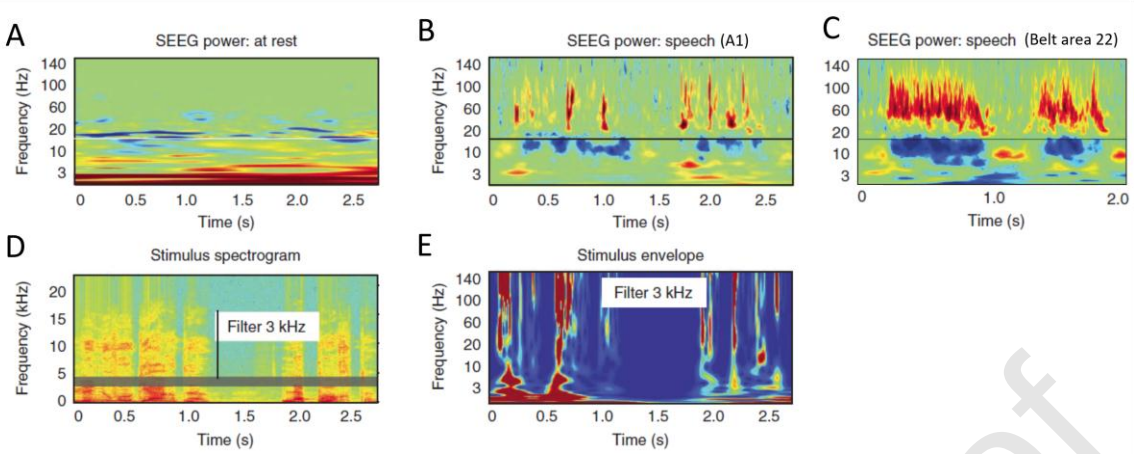


Figure 6: the shape of the temporal envelope is nonlinearly transformed when generating a local EEG. Here, amplitude modulated noise at 4Hz, whose envelope is the dotted orange line, elicits several different types of evoked responses within the very same primary auditory cortex of a human patient. The top one is primarily steady state with little onset, except during the first cycle of the sound. The middle one is a combination of onsets to each repetition of the noise and steady state response; note that the onset tends to vanish at the third cycle, there is a neural adaptation. The bottom response is mostly onset in addition to high frequency fluctuations. The instantaneous phase of each evoked potential is therefore different between each curve and even each cycle of the AM noise as is the lag between the peak stimulus and the peak EEG (same dataset as in (Gourévitch et al., 2008)).

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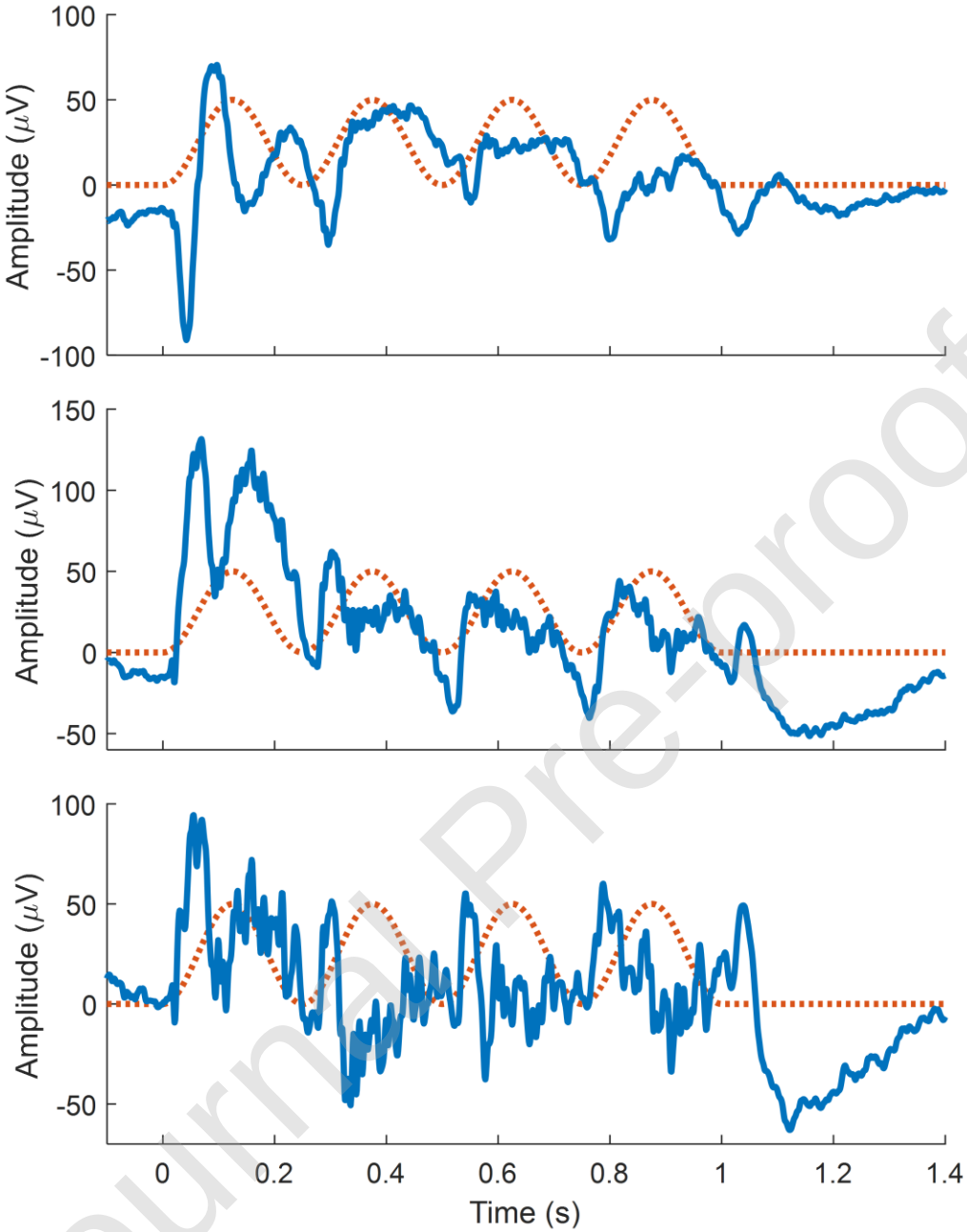


Figure 7. A simplified model of the role of oscillations in auditory processing. Neural entrainment (orange hatching pattern) prevails in the subcortical pathways and A1, building on phase-locking abilities of these areas. Gamma might be the only induced oscillation observed in A1 (blue squares) and would propagate bottom-up (green arrows), maybe subserving prediction error. As we go further in auditory associative areas, the relationship between neural entrainment and oscillations in low-frequency becomes ambiguous ("?") due to the difficulty to mathematically dissociate the two and because of the many top-down modulations from other fronto-parietal areas. All types of oscillations are observed in the fronto-parietal areas even during auditory tasks but would mainly serve at top-down modulating the excitability of the

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auditory cortex for the purposes of predictive coding and timing. With bottom-up Gamma, these top-down modulations would thus constitute a real-time input/output prediction loop between auditory cortex and fronto-parietal networks. The dissociation between these two latter networks would partly be based on distinct neural codes and in particular different use of coincident spiking activity ranging from rather event-related in subcortical auditory pathways and A1 to more network-related in higher-order areas (grey triangles)., correlating with a transition from evoked to more induced oscillations (blue triangles).

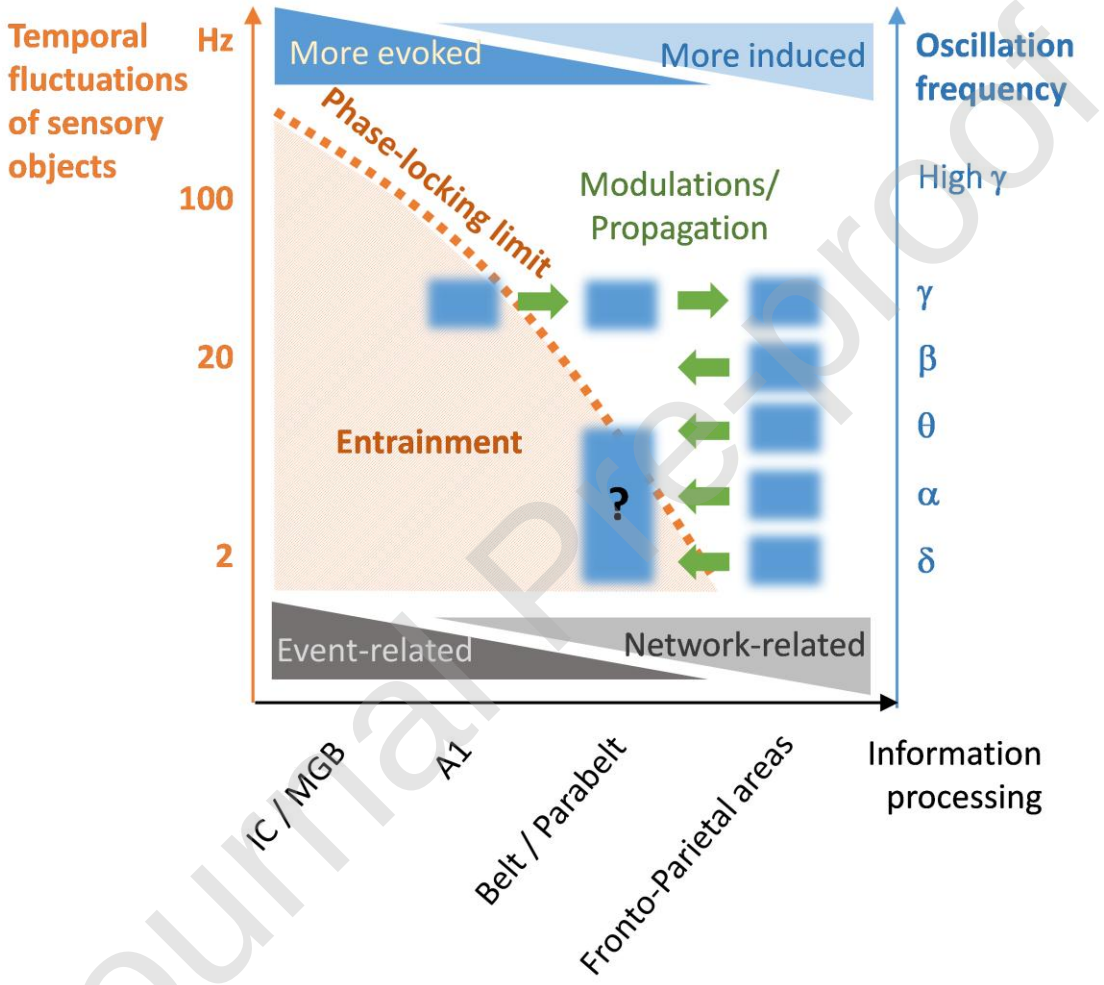


Fig. 8: Oscillations recorded from EEG. Adapted from (Malmivuo and Plonsey, 1995).

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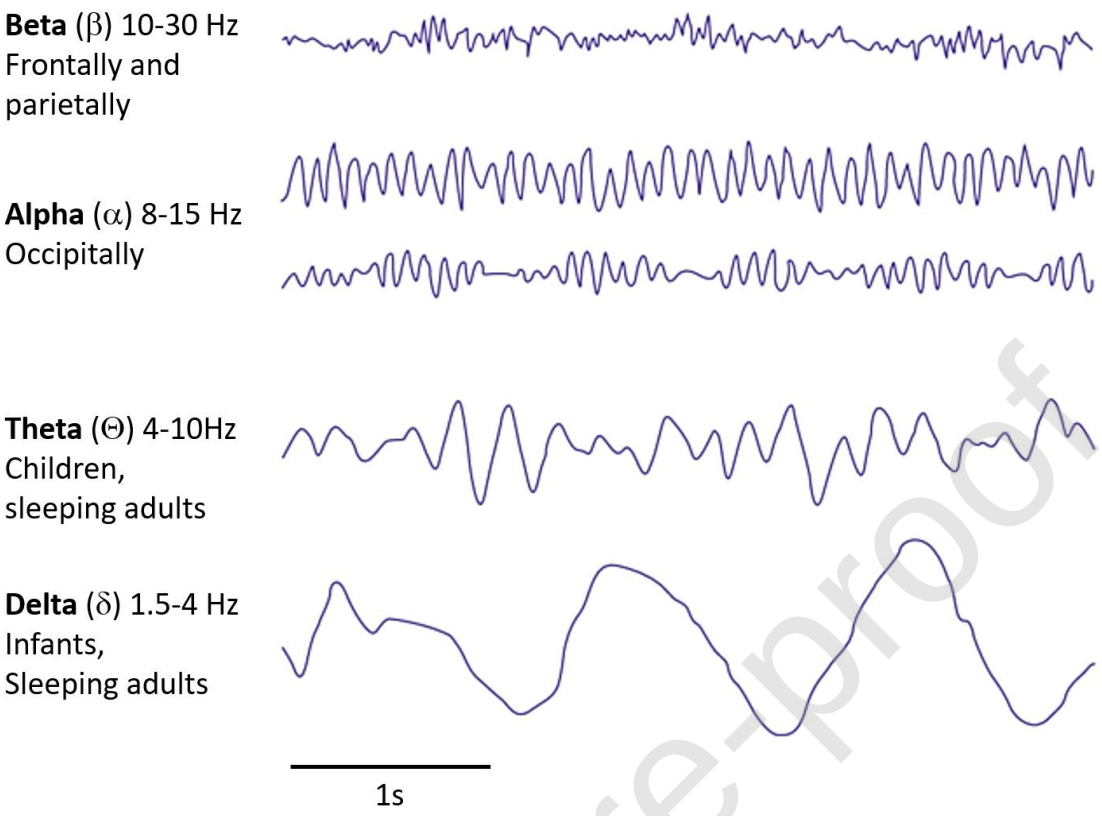
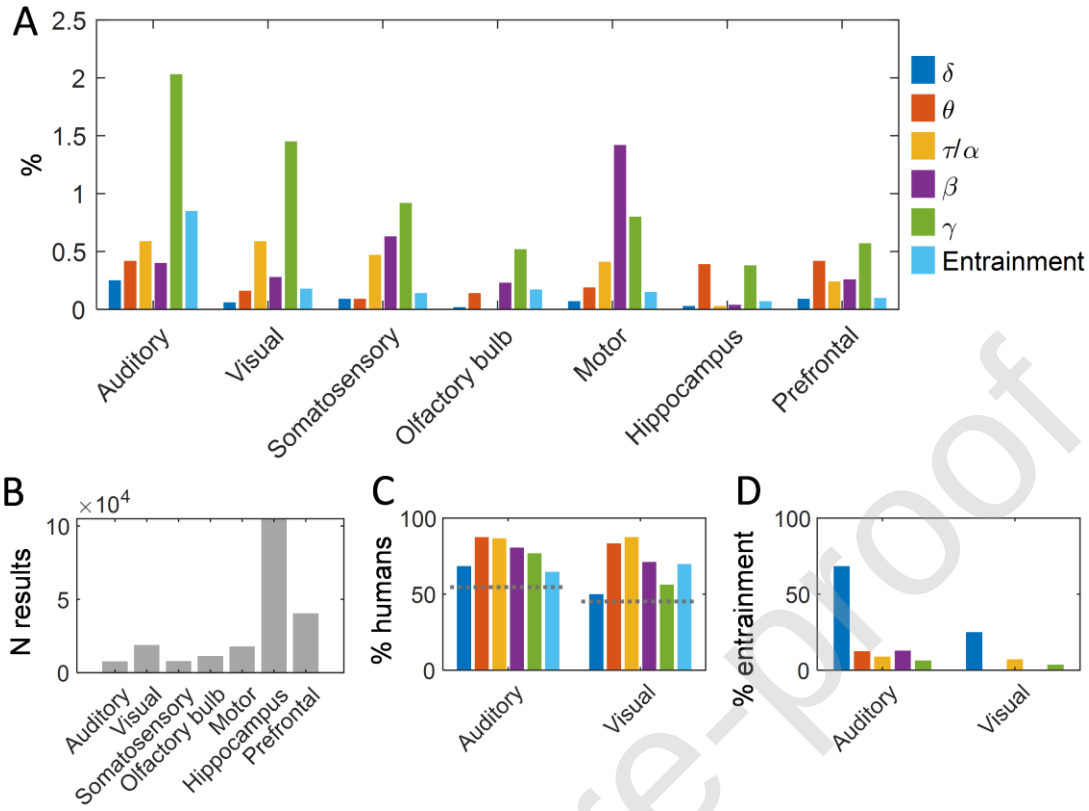


Figure 9. Pubmed records emphasize the imbalance in the presence of specific frequency bands between several cerebral areas as well as the imbalance between human and animal studies. **A.** Relative importance in percentage of publication records (Pubmed) about neural oscillations or entrainment in several areas of the central nervous system. Search example: (alpha oscillations[Title/Abstract]) OR (alpha band[Title/Abstract]) AND (auditory cortex[Title/Abstract]). **B.** Total number of publication records for the areas shown in A. Search example: (auditory cortex[Title/Abstract]). **C.** Percentage of publication records in humans among human+animal studies in the auditory cortex (left) and visual cortex (right). Search example: {same as in A} AND/NOT (human OR patients OR participants[Title/Abstract]). **D.** Percentage of publication records including "entrainment" in the auditory cortex (left) and visual cortex (right) per frequency band. Search example: {same as in A} AND/NOT (entrainment[Title/Abstract]).

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