INTRODUCTION

We experience the world through our sensory systems as what appears like a continuous stream of perceptual input. However, a range of psychophysical observations cannot easily be brought in alignment with such a view. For example, we perceive stimuli that are presented in short succession below a certain inter-stimulus interval (ISI) as simultaneous (Hirsh & Sherrick, 1961; Kristofferson, 1967; Lichtenstein, 1961) or as an ambiguously moving object.
Such apparent motion phenomena have been described already at the beginning of the last century (e.g., Wertheimer, 1912). Another example many of us know from everyday experience, is the so-called wagon-wheel illusion. The illusion describes the effect that the intermittent presentation of turning wheels or propellers of a plane (e.g., in a movie) results in a perception of movement in the opposite direction (Purves et al., 1996). The effect arises from a mismatch between the speed of the movement and the rate at which images of the movement are sampled. Strikingly, the illusion occurs even in the absence of intermittent presentation under constant lightning conditions (Purves et al., 1996). Thus, in contrast to our experience, our brain may be discretely sampling inputs to our sensory systems.

The idea that human perception may underly a discrete sampling process has been a matter of discussion for more than a century (VanRullen & Koch, 2003) and inevitably prompts the question by which mechanisms such discretization is implemented in the brain. It has been suggested that neural oscillations may play a key role by offering distinct temporal windows of cortical excitability and inhibition (Jensen & Mazaheri, 2010; Klimesch et al., 2007; VanRullen & Koch, 2003). For a long time, oscillations in the alpha band (~8–12 Hz) of the electroencephalogram (EEG) have been in the spotlight of investigation. Early on, the interest of researchers was captured by the similarity of the alpha oscillation’s cycle duration and the time-intervals between two stimuli required to cause/not-cause their apparent simultaneity (Kristofferson, 1967). More recent research found the detection of visual targets to be rhythmically modulated at a rate ~4 and 8 Hz depending on the number of objects to be sampled (Fiebelkorn et al., 2013; Landau & Fries, 2012; Re et al., 2019). It has been suggested that visual input is acquired by a global sampling process operating at ~8 Hz which distributes its sampling cycles over the to be processed objects resulting in lower sampling rates for multi-object scenarios (Fiebelkorn et al., 2013; Landau & Fries, 2012; Re et al., 2019).

With the advent of increasingly sophisticated computational analysis tools to process signals in the EEG or the magnetoencephalogram (MEG), it was possible to investigate the relationship between alpha oscillations and perception more closely. For example, negative associations between the detection or discrimination of visual stimuli and the power of pre-stimulus alpha oscillations in the visual cortex have been repeatedly reported (Ergenoglu et al., 2004; Hanslmayr et al., 2005, 2007; van Dijk et al., 2008). Similar relationships have been encountered in somatosensory perception (Baumgarten et al., 2016; Weisz et al., 2014; Zhang & Ding, 2010). While these results indicate that alpha oscillations are involved in gating information flow into sensory systems, specifically by inhibiting (task-irrelevant) inputs, alpha power fluctuations occur at time scales much larger than the aforementioned perceptual phenomena. The alpha cycle itself, however, appears to fit these timescales very well. So, in addition to the general inhibition of brain regions, excitability may additionally vary along the phase of the alpha cycle (Figure 1a). Indeed, in an early study Varela et al. (1981) presented participants with sequentially flashing LEDs and asked them to discriminate if the flashes appeared simultaneous, in motion or sequential. After fixing participants’ ISIs such that discrimination between two of these percepts was at chance level, they observed that the probability for experiencing one of the percepts depended on whether stimuli were presented locked to the positive peak or negative through of an ongoing alpha oscillation. In line with these results, later studies reported strong clustering of alpha phase around opposite phase angles for hits and misses in near-threshold visual target detection (Busch et al., 2009) and backward masking (Mathewson et al., 2009) tasks (see Figure 1 for an illustration of the general concept and pattern of results). A particularly elegant approach to investigate this relationship has been applied in a study which assessed the role of the alpha phase on the perception of phosphenes, an illusory percept that was directly evoked in the visual cortex by means of single-pulse transcranial magnetic stimulation (TMS; Dugue et al., 2011). This approach allows to bypass the time-delay arising from the neural transmission from the perceptual organs to the primary sensory area, thus allowing to directly map phase values related to inhibition and excitation along the oscillatory cycle. Results of that study suggested that the highest likelihood of phosphene perception occurred when it was elicited around the positive peak of the alpha oscillation (Dugue et al., 2011). Similar effects that depend upon the alpha phase have been reported in the somatosensory system (Ai & Ro, 2014). In the auditory domain, a broader range of low-frequency oscillations has been implicated in the implementation of phasic inhibition, covering frequencies in the delta (<4 Hz), theta (~4–8 Hz), and alpha range (Henry et al., 2014; Henry & Oleser, 2012; Lakatos et al., 2005; Ng et al., 2012; Strauss et al., 2015). Of great interest in the human auditory system is, of course, the role of phasic inhibition/excitation in the context of speech perception. It is known that slow oscillations (<10 Hz) in the auditory cortex follow the envelope of auditory scenes, particularly speech, which falls into the same frequency range. It has thus been suggested that these oscillations temporally align excitability in the auditory cortex to the meaningful aspects of the incoming speech signal (Giraud & Poeppel, 2012; Figure 1c). This phenomenon has also been referred to as entrainment of intrinsic brain activity to the speech signal, although this terminology has been criticized, as speech is not strictly rhythmic, violating core assumptions about synchronization phenomena from dynamic systems theory (Haegens, 2020; Meyer et al., 2019; Pikovsky et al., 2003).
Apart from the role of low-frequency oscillations, auditory cortex prominently exhibits oscillatory activity in the lower gamma range (around 40 Hz), which coincides with the ability to detect small gaps in noise and has, therefore, been hypothesized to determine the temporal resolution of the auditory system (Baltus & Herrmann, 2015; Pantev et al., 1996; Picton et al., 2003; Zaehle, Lenz, et al., 2010). In particular, participants are able to detect smaller gaps in noise, with higher individual gamma frequencies in the auditory cortex (Baltus & Herrmann, 2015).

From a global perspective, the above examples seem to indicate that neural oscillations in different frequency ranges may implement a ubiquitous mechanism of pulsed inhibition/excitation cycles that can control perceptual sampling. However, a couple of studies have challenged these results in recent years, reporting links between the power, but not the phase of pre-stimulus oscillations and visual perception (Benwell et al., 2017; Chaumon & Busch, 2014; van Diepen et al., 2015; Ruzzoli et al., 2019). Particularly noteworthy is a study by Ruzzoli et al. (2019). These authors attempted to replicate previous findings of the phasic modulation of perception by alpha oscillations in a pre-registered study. They could find associations between alpha power and perception but report evidence in favor of the null hypothesis with respect to the role of phase (Ruzzoli et al., 2019). There is, however, an interesting pattern between those null findings and previous studies that report the effects of oscillatory phase on perception in terms of the employed tasks. While the former mostly employ discrimination tasks (van Diepen et al., 2015: rotation angle/pitch of stimuli; Benwell et al., 2017: luminance; Ruzzoli et al., 2019: grating in gaussian white noise versus white noise only), the latter utilized detection paradigms in which a target stimulus that had to be detected was either present or absent (Ai & Ro, 2014; Busch et al., 2009; Dugue et al., 2011; Henry & Obleser, 2012; Mathewson et al., 2009). The only exception is the study by Chaumon and Busch (2014), which utilized the exact same task as Busch et al. (2009), yet with a different analysis strategy.

A fundamental limitation of M/EEG evidence, which all of the above is based on, is their correlational nature; i.e., oscillatory activity is observed as a function of experimental parameters, leaving ambiguous if the activity pattern (here the neural oscillation) under investigation implements the mechanism of action or reflects an epiphenomenon of the underlying neural processing (Herrmann, Strüber, et al., 2016). In order to demonstrate a causal involvement, one needs to reverse the experimental design by manipulating the brain oscillation under investigation and monitor the resulting changes in behavior as the independent variable (Herrmann, Strüber, et al., 2016). A promising way to achieve such modulation of neuronal oscillations is the use of rhythmic non-invasive brain stimulation (NIBS) via rhythmic transcranial magnetic stimulation (rTMS) or transcranial alternating current stimulation (tACS). By targeting specific properties of human...
brain oscillations such as power, frequency, and phase, these methods allow to study their distinct causal roles. Increasing or decreasing an oscillation’s frequency or changing its phase relation relative to stimulus presentation should give rise to specific changes in perceptual phenomena under the discrete sampling hypothesis.

2 PRINCIPLES OF (RHYTHMIC) NON-INVASIVE BRAIN STIMULATION

Before reviewing studies that applied rhythmic NIBS to investigate discrete sampling in perception, we will provide an introduction to the fundamental principles by which rTMS and tACS are thought to modulate neural oscillations.

Both methods intend to induce electric fields in the brain, which modulate the membrane polarization of neurons in the underlying tissue. With tACS, this is achieved by directly applying weak, alternating (usually sinusoidal) currents to the scalp via two or more electrodes (Woods et al., 2016). TMS, in contrast, works via the principles of electromagnetic induction (Barker et al., 1985; Hallett, 2000; Wagner et al., 2009). A major difference in the two methods lies in the electric field strengths they are able to create inside the brain. The membrane polarization achieved by a single TMS pulse is sufficiently strong to change neural excitability and even elicit action potentials (Wagner et al., 2009), whereas during tACS only a small proportion of the current reaches the brain, while the rest is shunted through the highly conductive skin (Vöröslakos et al., 2018). Consequently, the resulting polarization of neural cells by tACS is more subtle than that achieved with rTMS.

Despite their differences in terms of field strengths, it is believed that both methods can modulate brain oscillations via the rhythmic modulation of membrane polarization giving rise to neural entrainment (Herrmann et al., 2013; Reato et al., 2013; Thut, Schyns, et al., 2011). Entrainment refers to the process by which oscillating systems synchronize to each other, i.e., adapt in frequency and phase. Such synchronization is a ubiquitous physical phenomenon that can be observed in a multitude of natural and artificial (i.e., technical) oscillatory systems (Pikovsky et al., 2003). The fundamental prerequisite for entrainment to occur is the presence of a so-called self-sustained oscillator. The term describes a system with an internal energy source exhibiting rhythmic activity at a preferred intrinsic frequency (Eigenfrequency) until the energy source is consumed (Pikovsky et al., 2003). If such oscillators are weakly coupled with an external driving force with a frequency similar to their Eigenfrequencies, they synchronize their rhythmic activity (Pikovsky et al., 2003). Such coupling can be bidirectional (e.g., if two similar oscillators are adapting to each other) or unidirectional (a strong rhythmic force drives a weaker oscillation). The latter would be the case for rTMS and tACS where rhythmic stimulation is supposed to affect rhythmic neuronal activity but not vice versa. A crucial parameter that determines the strength of entrainment is the difference between the Eigenfrequency of the oscillator and the frequency at which the oscillator is perturbed by the driving force. The smaller the frequency difference, the smaller the amount of energy needed to entrain the oscillator. Conversely, with larger frequency difference, stronger perturbations are required to drive the oscillation. The triangular shape that arises when entrainment strength is displayed against the inverse relationship between frequency difference and intensity has been termed the “Arnold tongue” (Pikovsky et al., 2003; Figure 2a).

Evidence that rTMS and tACS are can entrain neural oscillations is largely based on in-vivo and in-vitro animal studies and computer simulations (Ali et al., 2013; Fröhlich & McCormick, 2010; Herrmann, Murray, et al., 2016; Johnson et al., 2019; Krause et al., 2019; Negahbani et al., 2018; Ozen et al., 2010; Reato et al., 2010). These suggest that external oscillatory currents can temporally align neural firing and shift the frequency and phase of local field potentials which give rise to large-scale oscillatory activity as seen in the M/EEG. Directly observing entrainment to transcranial stimulation in human electrophysiology is, however, challenging due to massive electromagnetic artifacts elicited by the stimulation, which heavily corrupt M/EEG signals (for a recent review see Kasten & Herrmann, 2019). To circumvent the problems of corrupted signals during stimulation, many human studies, especially on tACS, focused on monitoring effects after stimulation is switched off (Venierio et al., 2015). These so-called offline or after-effects have been observed after single sessions of rTMS or tACS and can outlast stimulation by several minutes up to few hours (Kasten et al., 2016; Schindler et al., 2008; Schutter et al., 2001; Wischnewski et al., 2019) and have been linked to changes in behavioral measures (Kasten & Herrmann, 2017). There seems, however, to be a difference with respect to the frequency specificity of both methods. During tACS, a (depending on the hardware in use) relatively pure sine wave is applied, to mimic oscillatory brain activity. This waveform contains most of its energy directly at the stimulation frequency. The brief pulses applied during rTMS, in contrast, although applied at a specific rate, have broadband spectral energy (Herrmann et al., 2013). Indeed, aftereffects of tACS seem to be more specific to the stimulated frequency band, while rTMS effects tend to be more widespread (Venierio et al., 2015). Although these results support the idea that both methods are able to modulate human brain oscillations, it has to be emphasized that online and offline effects of stimulation may not be based on the exact same mechanisms. Whereas rTMS and tACS online
effects are assumed to rely on the principles of entrainment, the minute to hour long aftereffects seem most likely to arise from NMDA-receptor mediated spike-timing-dependent plasticity (STDP; Vossen et al., 2015; Wischnewski et al., 2019; Zaehle, Rach, et al., 2010). The principles of entrainment allow rhythmic stimulation to entrain oscillatory phase, frequency, and power during stimulation. However, after stimulation is switched off, the endogenous oscillator should quickly fall back to its own preferred frequency and phase (Pikovsky et al., 2003) and only the elevated oscillatory power persists due to STDP (Kasten et al., 2016; Vossen et al., 2015; Wischnewski et al., 2019). As frequency and phase are the essential properties of interest for discrete sampling processes, these can only be studied during stimulation, but not thereafter.

3 | PROBING THE ROLE OF BRAIN OSCILLATIONS FOR DISCRETE SAMPLING

In principle, two main approaches can be differentiated in the study of brain oscillations for discrete sampling via rhythmic NIBS. On the one hand, brain stimulation can be applied to control the phase of the intrinsic oscillation. As parameters of the external driving force are under experimental control, sensory stimuli can be delivered systematically relative to its different phases (Figure 2b). Under the assumption that the phase of the intrinsic oscillation adapts and follows the phase of the external driving force at the time of

**FIGURE 2** Principles of entrainment via rhythmic non-invasive brain stimulation. (a) The “Arnold tongue” describes the relationship between the frequency deviation of a driving force to a self-sustained oscillator and the intensity required to entrain the oscillator. The larger the deviation, the higher the intensity that is required. (b) EEG oscillation synchronizes to external stimulation. With the onset of stimulation, the oscillation adapts to the external force in frequency and phase. As the stimulation should also cause higher synchronous neural activity, an increase in amplitude is additionally expected. Once the endogenous brain oscillation is synchronized to the external driving force, its frequency and phase can be derived from the known properties of the stimulation method, e.g., the interstimulus interval (ISI) of the rTMS pulses or the frequency and phase of the tACS waveform. Based on this information, the timing of sensory stimuli (e.g., brief light flashes) can be experimentally manipulated, i.e., presented at specific time points relative to the driving force. (c) Alternatively, stimulation can be used to speed up/slow down the oscillation of interest to change the temporal threshold for the occurrence of certain perceptual phenomena. In this example, two brief light flashes are presented at a fixed ISI. Under the assumption that the oscillation implements a discrete sampling process, these flashes should be perceived as simultaneous if the oscillation is slowed down, such that they fall into the same oscillatory cycle. Conversely, if the oscillation is speeded up, the same two stimuli should be perceived as sequential as the visual scene is sampled at a higher rate such that the two flashes fall into distinct cycles of the oscillation.
stimulus presentation. On the other hand, NIBS can be used to shift the frequency of the oscillation of interest by applying stimulation at a slightly higher or lower frequency as compared to the intrinsic oscillation in the brain. If the oscillation under investigation provides temporal windows of inhibition and excitation, an increase in frequency should lead the sampling process to operate at a higher rate, while decreasing the frequency should lead to sampling at a lower rate. As a result, the critical time intervals for certain perceptual phenomena, like simultaneity perception, to occur should be shifted into predictable directions (Figure 2c).

### 3.1 | Manipulating Phase

A variety of studies aimed to directly examine the role of phase by manipulating stimulus timing relative to the tACS phase or the timing of rTMS pulses.

In the visual domain, phase-dependent effects of rhythmic brain stimulation have been reported during the application of tACS and rTMS (Helfrich et al., 2014; Jaegle & Ro, 2014). Jaegle and Ro (2014) varied the onset of visual stimuli in a backward masking task relative to the offset of brief trains of 10 Hz rTMS applied over the right posterior parietal cortex. Participants ability to discriminate between the two target stimuli systematically varied depending on the temporal relationship between the offset of the last rTMS pulse and the onset of the target stimulus. In particular, discrimination performance was highest when the target stimulus was presented 100 ms after rTMS offset, such that rTMS pulses and stimulus fell into the same phase of a 10 Hz oscillation (Jaegle & Ro, 2014). In the same year, Helfrich et al. (2014) reported a phase-dependent modulation of target detection in a visual oddball paradigm during the application of 10 Hz tACS targeting occipital/parietal cortex.

Gundlach et al. (2016) carried out a tACS study following the same rational as the above examples, but bi-laterally targeted somatosensory instead of visual cortices at individual mu-alpha frequency. In that study, the detection of near-threshold electric stimuli applied to the index finger significantly depended on the phase of the mu-tACS waveform. Critically, in a control experiment, the authors did not find such an effect when targeting occipital alpha oscillations, indicating distinct roles of alpha/mu phase for the different modalities (Gundlach et al., 2016). While this result suggests similar roles for somatosensory mu-alpha and visual alpha oscillations, it has recently been argued that the mu-rhythm may implement pulsed excitation, while posterior alpha oscillations reflect pulsed inhibition (Bergmann et al., 2019).

Besides research on the role of phase in the alpha frequency range, several studies also investigated the role of other low-frequency oscillations in the implementation of phasic inhibition/excitation, especially in the auditory system and in the context of speech perception. Riecke, Formisano, et al. (2015) presented near-threshold click trains at the same frequency but varying phase lags relative to bilateral theta-tACS (4 Hz) over auditory cortices. Similar to previous reports in the alpha-band, participants’ ability to detect these clicks systematically varied depending on their phase relation to the 4 Hz tACS waveform. Similar phasic modulation of RTs during 4 Hz tACS was subsequently also found for more complex auditory stimuli (detection of randomly occurring rhythmic streams of musical cords fluctuating at the same frequency as tACS) (Riecke, Sack, et al., 2015). In the context of speech perception, several recent studies applied tACS using the envelope of a speech stream as the stimulation waveform, or modulated speech streams such that their envelopes match a sinusoidal tACS waveform. These studies aimed to enhance speech perception in the noise and segregation of two simultaneously occurring speech streams (Kadir et al., 2020; Riecke et al., 2018; Zoefel et al., 2020). In these experiments, speech perception was altered depending on the lag between the envelope tACS and the speech stream. In a subsequent study, the speech envelope was specifically filtered in the delta or theta range before being used for stimulation. In that study, stimulation with the oscillatory components of the speech envelope in the theta, but not in the delta range modulated speech perception (Keshavarzi et al., 2020).

Recently, two studies investigated the role of tACS phases outside the alpha range in the visual domain. Battaglini et al. (2020) investigated if tACS at beta frequency modulates visual crowding. While the authors found indications that task performance was modulated by beta power, there was no significant modulation of task performance with the phase of the tACS waveform (Battaglini et al., 2020). Somer et al. (2020) applied tACS in the theta frequency range concurrently with visual flicker (target stimuli changing color at the same frequency as tACS). When tACS was applied in-phase with the visual flicker, RTs needed to discriminate the flickering target stimuli were reduced as compared to anti-phase stimulation. The effect was specific to occipital cortex stimulation (i.e., did not occur during the stimulation of the dorsolateral prefrontal cortex). Interestingly, the effect did not occur when the experiment was repeated with stimulation at alpha frequency (Somer et al., 2020).

### 3.2 | Phase-Dependent Modulation of Brain Activation

The studies presented in the previous section reported phase-specific effects of rhythmic non-invasive brain stimulation on performance in different perceptual domains. Naturally, one would expect that the phasic modulation of perception is accompanied by changes in the underlying brain activity. However, thus far only a few studies addressed this question.
by combining rhythmic brain stimulation with neuroimaging approaches, particularly fMRI and MEG.

The blood-oxygen-level-dependent (BOLD) response is commonly used as one such marker of brain activation. Using sparse fMRI, Zoefel et al. (2018) observed the BOLD-response to speech perception to be modulated depending on the phase relationship between the speech stream and the tACS waveform applied at delta (~3.1 Hz) frequency over the left auditory cortex. In a similar vein, Herring et al. (2019) concurrently recorded MEG during the application of alpha-band tACS, while participants performed a visual rotation detection task combined with the presentation of inward moving gratings. The latter are known to induce a strong oscillatory response in the gamma range. Gamma oscillations show an antagonistic relation to low-frequency oscillations, especially in the alpha band (Boyle & Frohlich, 2013; Jensen & Mazaheri, 2010) and are hypothesized to signal conscious perception and active information processing (Gruber et al., 1999; Siegel et al., 2008; Wyart & Tallon-Baudry, 2008) and can, therefore, serve as a marker of brain activation. Using signal processing strategies to suppress the strong electromagnetic artifact elicited by the stimulation (Kasten & Herrmann, 2019; Neuling et al., 2015), the authors were able to show that the induced gamma-band response was modulated in a phase-dependent manner along the cycle of the alpha tACS waveform (Herring et al., 2019).

### 3.3 Manipulating Frequency

In comparison to controlling the oscillatory phase relative to stimulus timing, the modulation of frequency constitutes a more indirect way to test for the involvement of neural oscillations in these processes. Nevertheless, these approaches can provide interesting evidence for discrete sensory sampling and offer the advantage of allowing for more complex tasks, such as assessing whether or not critical time intervals for the occurrence of certain perceptual phenomena change depending on an oscillation’s frequency.

Cecere et al. (2015) used this approach to study the role of the posterior alpha peak frequency in cross-modal perception, specifically the occurrence of the sound-induced double flash illusion (Shams et al., 2002). The illusion describes the phenomenon that if two sound beeps are presented within ~100 ms together with one brief flash of light coinciding with the first beep, a second, illusory flash is perceived (Shams et al., 2002). Similar to other perceptual phenomena (illusory simultaneity: Allport, 1968; wagon wheel: Purves et al., 1996), the temporal window of the illusion is similar to the cycle duration of oscillations in the alpha band. After observing a correlation between participants’ individual alpha frequency (IAF) and the inflection point of the illusion (the interval between the two beeps at which the illusion occurs with a probability of 50%), the authors applied tACS below (~2 Hz), at, and above (+2 Hz) participants’ IAF. They found that the inflection point increased when participants’ IAF was slowed down and reduced as it was speeded up by tACS (Cecere et al., 2015).

Using a similar rational, Minami and Amano (2017) studied the role of alpha frequency for the perception of illusory jitter during motion induced, spatial conflict, occurring under low luminance contrast between moving objects (Arnold & Johnston, 2003). Again, after the authors observed correlations between participants’ IAF and the perceived jitter frequency, a variant of tACS using amplitude modulated waveforms (Negahbani et al., 2018; Witkowski et al., 2016) was applied below (~1 Hz) or above (+1 Hz) participants’ IAF to shift the oscillation’s frequency. Speeding up the IAF resulted in a higher perceived frequency of the illusory jitter, while slowing it down was found to decrease the perceived jitter frequency (Minami & Amano, 2017).

In the auditory domain, Baltus et al. (2018) applied tACS above (+4 Hz) or below (~4 Hz) participants’ individual gamma frequency aiming to modulate their auditory temporal resolution as assessed with an auditory gap detection task. While speeding up participants’ individual gamma frequency allowed them to detect shorter gaps in noise, tACS below the individual gamma frequency did not lead to the meaningful deterioration of auditory gap detection (Baltus, Wagner, et al., 2018).

### 3.4 Negative Findings

The previously mentioned experiments showcase successful attempts to link oscillatory frequency and phase to perceptual processes in different domains. However, there are also unsuccessful attempts to do so documented in the literature that should not remain undisputed. It should be noted, though, that due to the fact that negative results are often not published (prominently known as the file drawer problem), it is inherently difficult to obtain a full picture of unsuccessful attempts to use rhythmic brain stimulation in the modulation of perception (as in any field of research).

Recently, de Graaf et al. (2020) performed three visual target detection experiments with a tACS-phase-dependent stimulus presentation. In two of these experiments, participants had to detect grating stimuli briefly presented on a computer screen. In the third experiment, the target was a luminance change of a LED. During all three experiments, participants received tACS at their individual alpha frequency. In none of the experiments, a sinusoidal modulation of target detection depending on the phase of the applied tACS waveform was evident (de Graaf et al., 2020). However, in an exploratory analysis the authors found indications that tACS might have had a phase-dependent
effect on participants’ reaction times in the first two experiments (de Graaf et al., 2020). Following a similar rational, Sheldon and Mathewson (2018) employed a pulsed transcranial electrical stimulation protocol in an attempt to replicate previous findings of alpha phase-dependent effects on visual target detection. The pulsed stimulation is conceptually similar to rTMS stimulation, i.e., the endogenous brain oscillation is supposed to be driven by brief, rhythmic pulses, albeit using intensities comparable to other electrical brain stimulation methods (e.g., tACS, tDCS). The authors could not find an effect of the stimulus timing relative to the rhythmic electrical pulses on target detection in a visual backward masking task (Sheldon & Mathewson, 2018).

Erkens et al. (2020) recently tried to replicate the effects of envelope-tACS on speech perception. In that study, an initial effect of stimulation with the speech envelope vanished after the data were corrected for a learning effect in the sentence comprehension task used by the authors.

Concerning the manipulation of frequency, Baltus, Vosskuhl, et al. (2018) recently attempted to replicate the effect of increasing auditory temporal resolution by accelerating individual gamma frequency in a sample of normal-hearing elderly participants. On a group level, the authors did not observe the modulatory effect of tACS on auditory temporal resolution, previously found in a younger sample (Baltus, Vosskuhl, et al., 2018; Baltus, Wagner, et al., 2018). However, they found a positive correlation between the changes in auditory temporal resolution with participants’ individual gamma frequency in the experimental condition. This relationship was absent in the control group. The authors concluded, that only participants with low individual gamma frequency benefited from tACS, while those with already high individual gamma frequency did not, giving rise to only weak/absent effects on the group level (Baltus, Vosskuhl, et al., 2018).

While the above studies do not necessarily invalidate previous successful attempt to rhythmically modulate perception, they do highlight the need for further replication of these findings, as the number of studies on the matter is still relatively sparse and the experimental details that determine the occurrence and nature of effects are not well understood. For example, whether target detection or reaction times are modulated in a phasic manner may depend on the stimulus duration. Whereas previous studies that reported effects of alpha phase on detection rates used very brief stimuli in the range of 10–25 ms or below (Busch et al., 2009; Helfrich et al., 2014; Jaegle & Ro, 2014; Mathewson et al., 2009), de Graaf et al. (2020) presented target stimuli for 33.3 ms, which corresponds to ~1/3 of a full alpha cycle (100 ms at 10 Hz). It seems plausible that, if cortical excitability changes with the alpha cycle, for sufficiently long stimuli the phase may determine when the target is detected rather than if it is detected. This, of course, has to be confirmed in future experiments.

### 4 | METHODOLOGICAL CHALLENGES AND LIMITATIONS

As with every methodology, the use of rhythmic non-invasive brain stimulation approaches to study discrete sampling processes comes with a variety of limitations and methodological pitfalls, some of which are generally associated with the methods, others are directly related to the study of rhythmic perception. What at a glance may appear to be as trivial as connecting someone’s head to a battery by attaching some electrodes, becomes a highly complex issue in practice with a variety of potential pitfalls and sources of variability.

A general issue discussed in recent years is the relatively weak effects, especially encountered using transcranial electrical stimulation (e.g., tACS, tDCS), which repeatedly fail to replicate (Fekete et al., 2018; Horvath et al., 2015a, 2015b; Lafon et al., 2017; Veniero et al., 2017). This has recently led some authors to argue that the electric fields induced in the brain during stimulation may, in fact, be too weak to be able to entrain neural oscillations (Lafon et al., 2017; Vöröslakos et al., 2018) and that stimulation effects might rather be explained by peripheral mechanisms such as sensory entrainment via stimulation of peripheral nerves in the skin or the retina (Asamoah et al., 2019a; Schutter, 2016). However, conflicting with these ideas, recent work tested tACS effects more directly and found that electric fields produced during conventional tACS can entrain activity of single-neurons in the primate hippocampus (Krause et al., 2019) and that this effect persists if input from somatosensory nerves is blocked (Vieira et al., 2020).

Further, the electric field inside the brain, rather than in the periphery (skin and eyeballs) has recently been shown to be predictive of individual differences of tACS aftereffects (Kasten et al., 2019). Overall, these findings suggest that electric fields produced in the brain during tACS can be sufficiently strong to modulate oscillatory activity, although its efficacy may vary substantially across subjects. While peripheral stimulation might not be the primary mechanism of tACS, the possibility of entrainment via sensory pathways is an important confound that needs to be addressed by experimental designs and analyses (Asamoah et al., 2019b; Schutter, 2016). Whereas perceptual side effects like phosphenes and tingling sensations are relatively subtle during tACS and stimulation can be applied in silence, rTMS is accompanied by much stronger sensations and relatively loud clicks emitted during stimulation.
When discussing weak or absent effects of stimulation, it should be considered that individual variability can play an important role. Not every individual may react to brain stimulation in the exact same way or even at all. This can lead to situations where effects are weak or absent on the group level, while eliciting notable effects in a subset of individuals. A variety of factors have been identified that can potentially affect the susceptibility to brain stimulation. Among these factors are genetic differences, medication, age, and time of day (Krause & Cohen Kadosh, 2014; Ridding & Ziemann, 2010). Of potentially high significance are differences in individual head anatomy, which determine the exact location and strength of the current induced inside the brain and may thus strongly influence stimulation outcomes (Antonenko et al., 2019; Kasten et al., 2019; Laakso et al., 2015). Further, a variety of studies suggest that stimulation effects depend on the brain state during which the methods are applied. For example, some authors reported that tACS cannot further enhance the power of spontaneous alpha oscillations when participants have their eyes-closed or performed the experiment in darkness (which by itself causes a natural increase in alpha power), as compared to when they kept their eyes open and were seated in a dimly lit room (Alagapan et al., 2016; Neuling et al., 2013; Ruhnau et al., 2016; Stecher et al., 2017). Despite this potential ceiling effect, other studies also indicate that the oscillation of interest is nevertheless required to be involved in the respective brain state in order to be altered (Feurra et al., 2013; Kasten & Herrmann, 2017). This observation is in line with the principles of synchronization theory, which requires the presence of a self-sustained oscillator in order for entrainment phenomena to occur (Pikovsky et al., 2003). Unfortunately, the role which these aspects play in the context of modulating oscillatory phase and frequency has not been investigated yet, as many of the aforementioned studies were carried out using tDCS or focused on stimulation aftereffects and/or the power of the targeted brain oscillation. Nevertheless, for many of the factors (e.g., individual head anatomy, state dependency), it seems likely that they generally affect the efficacy of brain stimulation and thus affect the modulation of frequency and phase. For other factors, more closely related to the induction of aftereffects via neural plasticity, the impact on effects during stimulation (during which modulations of frequency and phase occur) may be less clear.

An important aspect to further address is the design of brain stimulation experiments aiming to investigate the role of brain oscillations in perception, particularly the choice of control conditions necessary to allow causal inference. The rationale of rhythmic NIBS is usually simplified along the lines of: if rhythmic stimulation at a given frequency modulates a certain behavior, then brain oscillations at that frequency serve a causal role for that behavior. However, underneath this simple cause-effect relation actually lies a complex causal chain (see Bergmann & Hartwigsen, 2020). A more accurate description would be that NIBS induces an electric field in a certain region of the brain, rhythmically shifting the membrane polarization of neurons in that region, which in turn gives rise to the entrainment of oscillations, which modulate behavior. From this more detailed description, one can already recognize that the first simplified statement contains some implicit assumptions about the location of the effect and the mechanisms of action (Bergmann & Hartwigsen, 2020). The most crucial among these is that rhythmic NIBS entrains endogenous brain oscillations. As discussed earlier, particularly for tACS this has yet to be demonstrated convincingly in humans and, in principle, alternative mechanisms of actions might be possible. For example, (Herring et al., 2019) recently suggested that the rhythmic fluctuations of membrane polarization may affect random brain activity in a rhythmic fashion without entraining endogenous oscillations at the applied stimulation frequency, although this hypothesis remains to be tested. Another concern is that the methods may elicit their effects via co-stimulation of sensory nerves, rather than direct stimulation of the brain. As indicated earlier, brain stimulation approaches can cause sensory perceptions as by-products. It is thus important to rule out that such sensory co-stimulation may artificially cause behavioral changes that can be misinterpreted as an effect of the oscillation under study. It is for example commonly reported that non-invasive brain stimulation elicits the perception of phosphenes (Kar & Krekelberg, 2012; Schutter, 2016), which, in case of rhythmic stimulation, themselves occur in a rhythmic manner. In the context of a visual task, these rhythmic phosphenes could in turn affect the detectability of near-threshold stimuli due to changes in the perceived background illumination, giving rise to phase-dependent modulation of detection performance independent of an actual modulation of the targeted brain oscillation. In order to rule out such confounds, if they cannot be avoided, one can use dedicated stimulation protocols aiming to stimulate the periphery (e.g., the retina), while minimizing the current arriving in the brain area targeted during the main experimental condition as additional control conditions.

In most studies, researchers aim to pinpoint the role of a specific property (i.e., frequency, power or phase) of a specific oscillation (i.e., in a specific frequency band) in a certain brain region for a given function. Rhythmic brain stimulation will, however, likely affect all three parameters at the same time. It is thus crucial to design stimulation experiments in a way that allows valid conclusions about the origin of effects. When the role of neural oscillations for discrete sampling is investigated, the interesting properties are the phase and the frequency of the oscillation and it has to be ruled out that the modulation of oscillatory power gave rise to the effects. Consider a case where stimulation is applied to shift the frequency of oscillation into a certain direction
and a change in a perceptual phenomenon is observed. This result on its own could, in principle, also be explained by a stimulation-induced change in oscillatory power. An additional control stimulation that would lead to a similar effect on power but shifts frequency into the opposite direction with a reversed perceptual effect (Cecere et al., 2015) could rule out such an explanation.

Similar rationales can be applied to the other aforementioned parameters (frequency band, location). If only applied to one particular brain region, it cannot be disentangled if an effect is specific to that region, or if it would also occur during the stimulation of other regions, which makes the inclusion of a control stimulation applied to at least one additional brain region desirable. Especially transcranial electrical stimulation is known to be spatially widespread rather than focal; i.e., due to volume conduction, current can propagate to many neighboring brain regions leading to their co-stimulation. This makes it difficult to pinpoint the role of small circumscribed regions. To further complicate the situation, distant brain regions may be indirectly co-stimulated via network interaction with the target region (Bergmann & Hartwigsen, 2020). The usage of high definition stimulation montages, utilizing multiple electrodes in combination with individualized, computational modeling of current distributions may, however, allow for more focal stimulation protocols in the future (Huang et al., 2018; Saturnino et al., 2019; Wagner et al., 2016). The same problem also applies to the specificity of frequency. An effect of stimulation in one frequency band does not preclude that similar effects may exist in other frequency bands, or that other frequency bands may be co-stimulated via their cross-frequency interactions with the target frequency (Palva et al., 2005) or harmonic entrainment (Herrmann, 2001).

Based on the above considerations, in an ideal world, one would design experiments using control conditions to account for all of the aforementioned aspects. However, in practice, this can be challenging as every new stimulation condition poses an additional burden for participants (longer experiments, experimental sessions on several days due to limitations in stimulation dosages that can safely be applied per day, etc.). Consequently, experimental conditions chosen for a specific research question often reflect a compromise including only conditions necessary to draw valid conclusions but not fully resolving all aspects of the specificity of an effect. Overall it should be emphasized, that due to these problems, stimulation approaches are not well suited as exploratory tools. Rather, they are most powerful when used in combination with prior correlational evidence from neuroimaging to further probe and extent these findings (Cecere et al., 2015). Future research may, at least in part, circumvent the problems of excessive numbers of control conditions by utilizing novel approaches that allow sampling large parameter spaces efficiently using Bayesian Optimization (Lorenz et al., 2017, 2019). The framework has recently shown to allow and efficiently (within ~5 min) determine tACS parameters that elicit the strongest phosphenes in a given montage among >190 possibilities (Lorenz et al., 2019).

Concerning the analysis of phase-dependent effects of rhythmic non-invasive brain stimulation, two articles have recently emphasized the importance of careful data analysis procedures. A problem when studying the role of phase for perception is the natural delay between the physical stimulus presentation and the arrival of the resulting neural signals in the primary sensory areas, which is subject to variability between individuals. As phase effects could cancel out due to this variability, many studies employed an alignment procedure (e.g., Busch et al., 2009; Neuling et al., 2012; Riecke, Formisano, et al., 2015; Zoefel et al., 2018). It has recently been emphasized that such alignment according to performance (e.g., individual phase bin with best/worst performance) can introduce a bias, because the distribution of data within the phase bin used for alignment is skewed and will increase false-positive rates if not excluded from the analysis (Asamoah et al., 2019a). The authors report that two out of six tACS studies on auditory perception did not account for this bias, leading to ambiguity whether their results reflect a real, stimulation induced, phase-dependent modulation of perception or an analytical bias. However, the remaining four studies corrected for the bias still found phasic modulation of auditory perception or rhythmic modulations of associated brain activity in the fMRI (Asamoah et al., 2019a). Another recent study demonstrated how learning effects can give rise to artificial stimulation effects if combined with certain analysis approaches and randomization/counterbalancing approaches if not accounted for (Erkens et al., 2020).

Thus far, there was no clear consensus on the best way to test for the phasic modulation of behavioral or physiological outcome measures. Many researchers designed individual strategies as part of their studies. Recently, Zoefel et al. (2019) compared the performance of a variety of analysis approaches to detect the phasic modulation of behavioral and physiological response variables documented in the literature in a simulation study. In addition, they assessed the role of experimental parameters such as the number of repetitions and phase bins going into the analysis. They consistently found linear (for continuous response variables; e.g., RTs) and logistic (for dichotomous response variables; e.g., hits versus. misses) regression models with circular predictors to model single-trial data to be most sensitive to detect phasic modulations of response variables (Zoefel et al., 2019). A particular advantage of the method is that it does not require phase-realignment in order to work, thus avoiding analytical bias without sacrificing a whole experimental condition (i.e., the removal of the phase bin used for re-alignment). Concerning the structure of experiments, the number of phase bins going into the analysis appeared less relevant to
the detection of effects as compared to the number of repetitions. Given that there is a limited amount of time each participant can be stimulated during an experiment, it seems more desirable to limit the number of phases at which stimuli are presented during stimulation in favor of more repetitions (Zoefel et al., 2019).

5 | A CAUSAL ROLE FOR BRAIN OSCILLATIONS IN DISCRETE PERCEPTUAL SAMPLING?

The core advantage of rhythmic NIBS over sole electrophysiological measurements is the possibility to establish causal relationships between brain oscillations and cognitive functioning, if conducted carefully, with appropriate controls and/or strong prior correlational evidence from neuroimaging (Bergmann & Hartwigsen, 2020; Bergmann et al., 2016; Herrmann, Strüber, et al., 2016). So naturally, the question remains whether, in the light of the limitations of the methods, rhythmic NIBS experiments did already establish such causal relations between discrete sampling processes in different modalities and neural oscillations in certain frequency bands.

Overall, there seems to be a pattern, that frequency bands for which correlational evidence had been obtained in a certain domain tend to be successfully used in rhythmic brain stimulation to modulate rhythmic perception (e.g., alpha in the visual domain: Helfrich et al., 2014; Jaegle & Ro, 2014; Minami & Amano, 2017, mu in the somatosensory domain: Gundlach et al., 2016, or theta in the auditory domain: Riecke, Formisano, et al., 2015; Riecke, Sack, et al., 2015). However, the number of studies performed in each sensory domain is still very sparse up to this point and further, ideally independent, replication of the effects is needed to increase confidence in the findings. In particular, it seems attractive to incorporate recent advances in individualized targeting (Huang et al., 2018; Saturnino et al., 2019; Wagner et al., 2016) and powerful analysis approaches (Zoefel et al., 2019) in these studies. In addition, variations in stimulus and task properties may foster our understanding under which conditions discrete sampling occurs and how generalizable the effects may be.

The most important factor to consider when discussing evidence for the causal involvement of brain oscillations in perception probably is the assumed underlying mechanism. The studies showcased in this review, heavily rely on the assumption that rhythmic transcranial stimulation entrains endogenous oscillations in the brain. While there are some studies in humans showing this for rTMS (Hanslmayr et al., 2014; Thut, Veniero et al., 2011; Zmeykina et al., 2020), the assumption is mostly based on animal and computational studies for tACS (Ali et al., 2013; Fröhlich & McCormick, 2010; Johnson et al., 2019; Krause et al., 2019; Negahbani et al., 2018). How far these findings can be translated to humans is still debated (Asamoah et al., 2019b; Lafon et al., 2017; Vöröslakos et al., 2018). This uncertainty about underlying mechanisms ultimately leads to a situation in which non-invasive brain stimulation can only provide evidence for causal involvement of brain oscillations in cognition and perception conditional on future confirmation that stimulation elicits its effects via the mechanisms of neural entrainment.

6 | CONCLUSIONS AND OUTLOOK

Rhythmic brain stimulation approaches have great potential for investigating the role of brain oscillations in the context of perceptual sampling. They offer a tool to probe for causal relationships and enhanced control over experimental parameters (e.g., the relation between stimulus presentation and oscillatory phase). The idea to use rTMS and tACS to entrain human brain oscillation is still rather new, the usage of this framework to probe the role of oscillations in the context of discrete sampling in perception even newer. Consequently, the number of studies perusing this approach is still sparse and their results may not be considered definitive and well established. Rather, these works provide first, interesting insights. It should be emphasized that the brain stimulation field is still on its way to understand the underlying mechanisms of the methods and to discover the problems and pitfalls associated with them. We currently see attempts to overcome these problems in multiple ways. Some research aims to enhance stimulation effects by individualizing stimulation protocols, e.g., by individually optimizing stimulation montages to maximize electric fields at the target side (Huang et al., 2018; Saturnino et al., 2019; Wagner et al., 2016) or adaptively optimizing stimulation parameters depending on an individuals’ brain activity (Bergmann et al., 2016). Other authors try to overcome stimulation artifacts in order gain insights into effects during stimulation to further understand underlying mechanisms (Helfrich et al., 2014; Kasten et al., 2018; Kohli & Casson, 2019; Neuling et al., 2015; Noury et al., 2016; Ruhnau et al., 2016; Voss et al., 2014), or try to understand determinants of an individuals’ susceptibility to stimulation such as brain state-dependency (Feurra et al., 2013; Neuling et al., 2013; Ruhnau et al., 2016) or genetic factors (Riddle et al., 2020). Future research in these domains can foster our understanding of the underlying mechanisms of non-invasive brain stimulation techniques and substantially increase their reliability.

Brain stimulation experiments have some advantages over mere electrophysiological measurements. Whereas the latter requires post hoc assignments of phase or frequency conditions, which can result in unbalanced or
skewed data distributions hampering subsequent statistical analyses, brain stimulation approaches offer control over these properties of the oscillation avoiding such problems and strengthen conclusions. Further, some properties such as the frequency of the oscillation of interest may not exhibit sufficient within-subject variability to correlate its impact on a certain perceptual effect. In such cases, rhythmic stimulation can be used to modulate this property into different directions within the same individual to circumvent this problem (Cecere et al., 2015). It should be emphasized though, that initial electrophysiological evidence provides crucial prior information to properly identify the stimulation target. Given the degrees of freedom in terms of stimulation montages and frequencies, a stimulation study carried out without this prior information is almost certainly doomed to fail. In combination, however, electrophysiology and rhythmic non-invasive brain stimulation can have huge potential to further extent our knowledge on the role of brain oscillations in perception.

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CSH holds a patent on brain stimulation. FHK declares no competing interests.

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