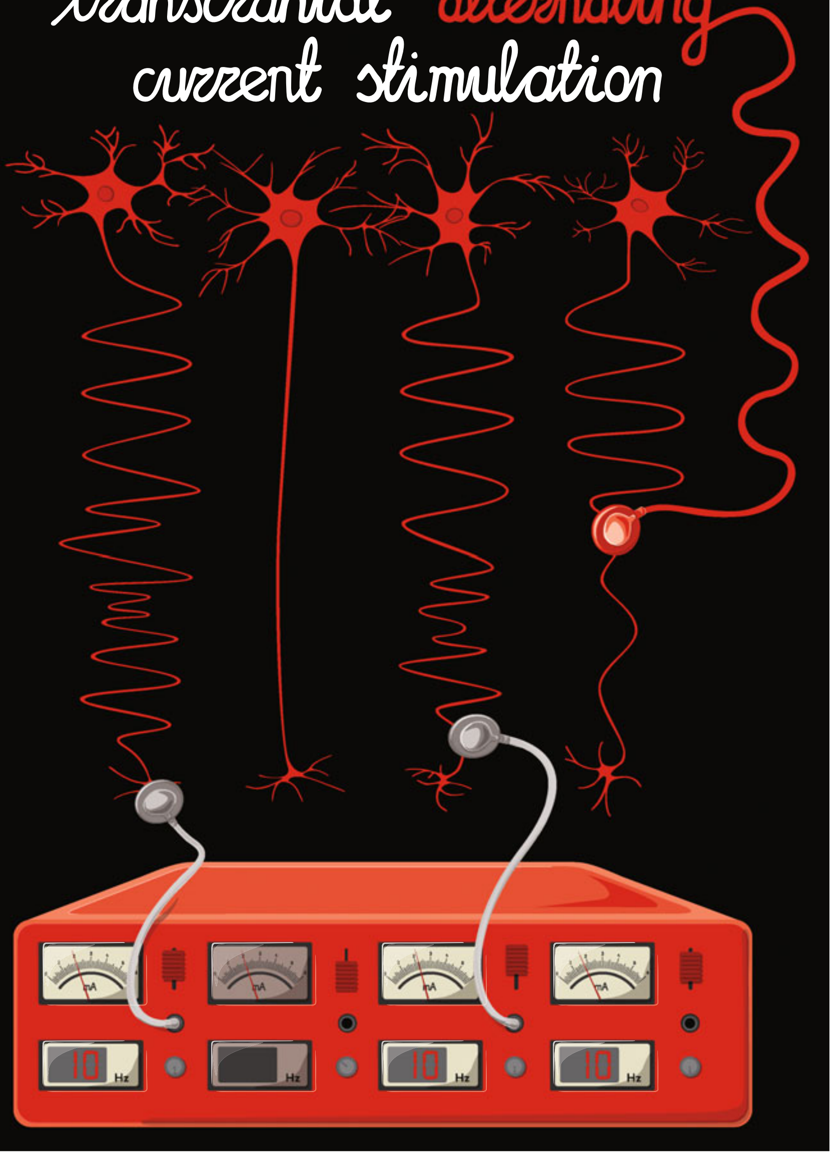
transcranial alternating current stimulation



Transcranial Alternating Current Stimulation

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Introduction

An important attribute of neuronal activity are oscillations that can be measured by electroencephalography (EEG) or magnetoencephalography (MEG; Fröhlich 2014; Thut and Miniussi 2009). The rhythmic oscillatory activity within and between different brain regions is thought to be causally linked to higher order cognitive abilities, such as attention, perception, cognitive control, and memory (Herrmann et al. 2015; Thut and Miniussi 2009). Transcranial alternating current stimulation (tACS) is a neural entrainment technique which influences the brain control on human action by modulation of brain oscillations (Antal and Paulus 2013). Similarly, to tDCS, see Chapter "Transcranial Direct Current Stimulation", tACS is a

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L.S. Colzato, *Theory-Driven Approaches to Cognitive Enhancement*,
DOI 10.1007/978-3-319-57505-6_10

"top–down" technique—that indirectly modulates subcortical activity through primary network changes in cortical activity. This technique is relatively cheap, comparably easy to conduct, and offers a reliable sham stimulation condition. Even though tACS is only in its beginnings, several studies have already supported the effectiveness of this technique to modulate and enhance cognitive functioning in healthy humans (for recent reviews see, Herrmann et al. 2015; Kuo and Nitsche 2015; Cohen Kadosh 2015; Fröhlich et al. 2014; Krause and Cohen Kadosh 2014; Antal and Paulus 2013). Notwithstanding the promising results gathered in this growing literature, more research is still needed to improve our understanding of the effects of tACS and to optimize protocols for future studies.

In this chapter, we provide a summary of the enhancing effects of tACS research on cognitive functions in healthy individuals. The primary aim of this chapter is to complement previous reviews (Herrmann et al. 2015; Kuo and Nitsche 2015; Cohen Kadosh 2015; Fröhlich et al. 2014; Krause and Cohen Kadosh 2014; Antal and Paulus 2013) so as to gain a better understanding of the conditions under which tACS has been found to be effective in enhancing cognitive functioning. First, we will describe the mechanism of action of tACS. Second, we will outline the recent available studies investigating the effect of tACS on various cognitive processes. The studies point out that tACS has promising potential for promoting memory, visual perception, motor learning, and creativity. Last, we will identify potential modulators of response to tACS.

Mechanism of Action

Similarly to transcranial direct current stimulation (tDCS), see Chapter "Transcranial Direct Current Stimulation", tACS protocols allow to deliver a weak electrical current to the scalp through two or more electrodes placed over areas of interest (Nitsche et al. 2008; Ruffini et al. 2013; Antal and Paulus 2013). However, while tDCS is used to induce a constant current flow that causes polarity-dependent effects on cortical excitability via tonic subthreshold polarization of neuronal membrane potentials, tACS is used to apply an oscillatory (sinusoidal) electrical stimulation of a specific frequency that modulate neuronal membrane potentials in a frequency-dependent manner (Fig. 1; Nitsche et al. 2008; Ruffini et al. 2013; Antal and Paulus 2013).

tACS is typically applied with stimulation intensities and durations similar to tDCS, and at oscillation frequencies within the EEG frequency spectrum (usually between 1 and 100 Hz). When applied within the typical EEG frequency spectrum, tACS does not seem to induce neuroplasticity but rather its primary effect seems to entail the modulation of spontaneous ongoing cortical oscillations (Antal et al. 2008). Specifically, tACS is assumed to be able to enhance cortical oscillations at frequencies close to the stimulation frequency and to entrain or synchronize neuronal networks (Reato et al. 2010, 2013; Antal and Paulus 2013; Ali et al. 2013; Helfrich et al. 2014b). However, when tACS is applied outside the typical EEG

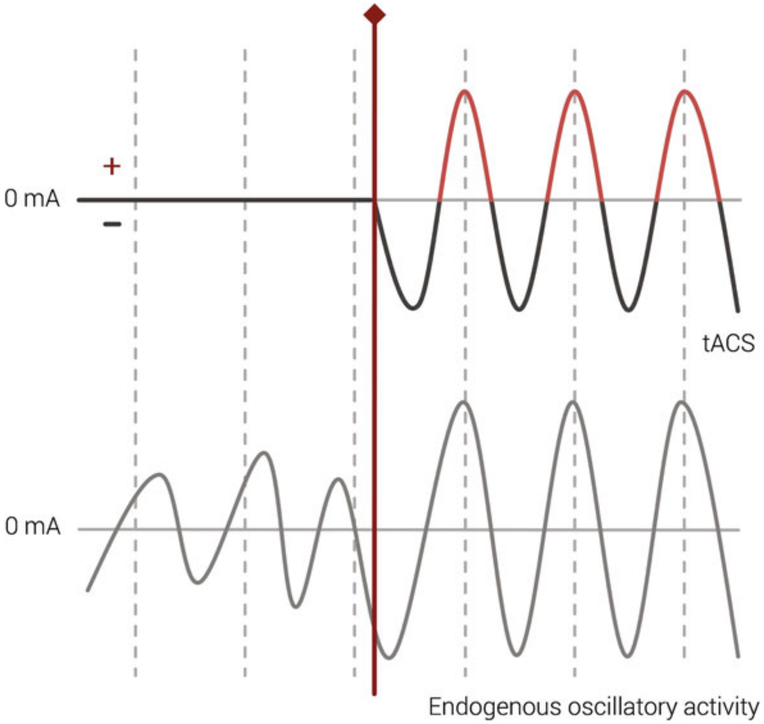

Fig. 1 In tACS two or more electrodes are used to apply an oscillatory (often sinusoidal) electrical current of a specific frequency to a targeted brain area. The *upper wave in the figure* shows how the sinusoidal wave oscillates around 0 mA. The applied current is hypothesized to entrain endogenous oscillatory activity to the frequency of the applied current, as shown in the *bottom part of the figure*. Therefore, endogenous activity becomes phase-locked with the applied current and gains power in the entrained frequency, as shown by higher amplitude

frequency range (e.g., at 140, 600 Hz, and in the low kHz range), tDCS-like neuroplastic excitability alterations are more likely to occur (Moliadze et al. 2010, 2012; Chaieb et al. 2011).

As tACS can interfere with naturally occurring cortical oscillations, this technique is suitable to probe the physiological and functional role of specific cortical oscillations in cognition, as the available findings indeed suggest (Herrmann et al. 2015; Kuo and Nitsche 2015; Cohen Kadosh 2015; Fröhlich et al. 2014; Krause and Cohen Kadosh 2014; Antal and Paulus 2013). Besides this, tACS can be used as an add-on tool to cognitive and/or motor training in order to optimize and enhance behavior.

However, more research is still needed to gain a better understanding of the physiological mechanisms of tACS and of the full potentialities of this technique. Online measurement of tACS effects via EEG or MEG monitoring is difficult due to artifacts induced by the stimulation. However, recent attempts aimed at separating neuronal activity from stimulation-induced artifacts corroborate the assumption of entrainment (Neuling et al. 2015; Helfrich et al. 2014b). In addition, a recent in vitro study has simulated in vivo-like 'endogenous' oscillations in a mouse cortical slice and showed that application of an oscillating electrical field enhanced these endogenous oscillations (Schmidt et al. 2014). This again provides evidence for entrainment, which may extend to tACS applied to the human brain (Schmidt et al. 2014).

Enhancing Effects in Working Memory, Visual Processing, Motor Learning, and Creativity

Previous studies on tACS have effectively used this technique to enhance a wide range of functions, including working memory (WM; Jaušovec and Jaušovec 2014; Jaušovec et al. 2014; Meiron and Lavidor 2014; Polanía et al. 2012) and visual processing (Helfrich et al. 2014b; Laczó et al. 2012). In terms of cognitive enhancement, WM is particularly important in order to counteract the effects of healthy aging. First, in a seminal study it has been shown that tACS-induced theta-synchronized activity between left posterior parietal cortex and dorsolateral prefrontal cortex improved visual memory-matching reaction times. In contrast, tACS-induced frontoparietal theta phase desynchronization deteriorated performance (Polanía et al. 2012). Second, active tACS with individually determined theta frequency applied to the left parietal (target electrode = P3) but not to the frontal (target electrode = F3) brain areas significantly increased WM storage capacity (Jaušovec and Jaušovec 2014). Further, in a similar study, besides stimulating left frontal and left parietal, the authors stimulated also the right parietal areas and the enhancing effect of theta tACS on WM executive processes was most pronounced for right parietal stimulation (Jaušovec et al. 2014). Moreover, Meiron and Lavador (2014) showed that theta tACS improved online WM accuracy when the bilateral dorsolateral prefrontal cortex was actively stimulated compared to sham stimulation. Finally, very recently, Vosskuhl et al. (2015) tested the assumed causal role of the gamma/theta ratio in sustaining higher order cognitive functions, such as WM and short-term memory (Lisman and Jensen 2013; Roux and Uhlhaas 2014). To this end, they applied tACS over the frontal cortex to increase the gamma/theta ratio while engaging the participant in two tasks: one tapping WM performance (i.e., the backward digit span task), and one short-term memory performance (i.e., the forward digit span task). Gamma/theta ratio was increased by reducing the theta frequency that showed best phase-amplitude coupling to a gamma-range frequency, such that one extra gamma cycle fit onto the theta cycle. Improved short term, but not WM performance was observed during tACS, which increased gamma/theta ratio—however, the effect vanished after tACS offset. In contrast, WM performance might depend on theta synchronization between frontal and parietal areas instead, as suggested by earlier research (Polanía et al. 2012).

In sum, all the studies described above point out to a crucial role of theta band activity for enhancing WM.

In terms of visual perception, 10 Hz tACS applied over the parieto-occipital cortex has been shown to increase parieto-occipital alpha activity and to synchronize cortical oscillators with similar intrinsic frequencies to the entrainment frequency. Most importantly, tACS was effective in enhancing target detection performance in a phase-dependent fashion underlying, therefore, the causal role of alpha oscillations for visual perception. Related to that, a recent study aimed to assess how tACS affects motion perception in healthy humans (Kar and Krekelberg 2014). 10 Hz tACS of the left human middle temporal/V5 complex (hMT/V5 +) improved visual motion direction discrimination performance and attenuated motion adaptation of visual stimuli presented in the contralateral hemifield. Importantly, tACS was effective only when applied during the adaptation induction phase (i.e., when the adapter was on the screen), but not when applied before visual stimuli were presented or during recovery from motion adaptation (i.e., when the screen was blank). Given that prolonged stimulus presentations (i.e., adaptation) typically cause a reduction in motion discrimination performance (Van Wezel and Britten 2002), it is reasonable to speculate that tACS may have counteracted such a reduction, thereby leading to increased sensitivity. Therefore, these findings can be taken to suggest that tACS can attenuate motion adaptation. Further, Cecere et al. (2015) used tACS to probe the role of occipital cortical oscillations in audio–visual integration, as indexed by the sound-induced double-flash illusion. In this illusion, the presentation of two beeps within about 100 ms together with one flash elicits the perceptual illusion of a second flash (Shams et al. 2000). Given that alpha-band oscillations are known to cycle every ~100 ms, tACS was delivered over the occipital cortex at either the individual alpha frequency (IAF)—previously estimated via task-concomitant EEG recording—or off-peak alpha frequencies (IAF ± 2 Hz). Results showed that compared to tACS at the IAF, tACS at slower (IAF − 2 Hz) and faster (IAF + 2 Hz) frequencies increased and decreased the temporal window of the illusion, respectively. These findings suggest that occipital alpha oscillations may represent the neurophysiological substrate enabling audio–visual interactions.

Beyond alpha, also gamma band activity plays an important role in visual perception. In another study, pertaining to illusory perception, Cabral-Calderin et al. (2015) investigated the differential role of alpha (10-Hz) and gamma (60- and 80-Hz) frequencies in the resolution of perceptual ambiguity. Participants performed a bistable perception task while the occipital cortex was stimulated via tACS to increase cortical oscillations in the tested frequencies. Results showed that 60-Hz tACS increased spontaneous perceptual reversal rates, while no effects were observed for alpha (10 Hz) and higher gamma (80 Hz) frequencies—this suggests that gamma but not alpha oscillations are causally involved in the resolution of perceptual ambiguity of bistable stimuli.

The number of tACS studies investigating possible enhancing cognitive processes apart from perception and WM is still relatively small, but the available findings are promising. Especially, interesting from a cognitive enhancement perspective are studies published very recently showing that tACS is effective in modulating motor learning and creativity. First, Pollok et al. (2015) tested the role of motor-cortical alpha and beta oscillations in motor sequence learning. tACS was applied over the left primary motor cortex while participants performed a serial reaction time task. Results showed that, compared to sham stimulation and tACS delivered at a control frequency of 35 Hz, both 10 Hz (alpha) and 20 Hz (beta) tACS facilitated the acquisition of a new motor sequence. Only 20 Hz tACS was found to stabilize the newly learned motor sequences immediately after acquisition. These findings partly replicate previous results reported by Antal et al. (2008) who observed implicit motor learning facilitation during 10-Hz tACS. Besides that, these results corroborate the hypothesis that motor-cortical beta oscillations may sustain and enhance motor control. See Chapter "The Application of Brain Stimulation and Neural Entrainment in Sport", for practical application of these results in sport science.

Second, Lustenberger et al. (2015) employed tACS to probe the causal role of prefrontal cortex alpha-band frequency activity (8–12 Hz) in divergent thinking—a style of creative thinking that allows the generation of innovative ideas. Results showed that 10-Hz, but not 40-Hz tACS delivered bilaterally over the dorsolateral prefrontal cortex during the execution of the Torrance Test of Creative Thinking (Baer 1993; Kim 2006) significantly improved task performance, compared to sham stimulation. This finding represents direct evidence for a causal role of prefrontal alpha oscillations in creative thinking, which is consistent with the conclusion of previous correlational studies (Fink et al. 2007; Fink and Benedek 2014; Jauk et al. 2012).

In sum, a growing body of evidence shows that tACS might enhance cognitive functioning by modulating rhythmic cortical activity within and between cortical areas. Specifically, theta tACS seems to support WM performance, whereas beta tACS sustains motor learning, and alpha and gamma tACS are more related to visual perception and creativity. Nonetheless, a full understanding of the factors influencing effects of this technique is still lacking (Battleday et al. 2014; Krause and Cohen Kadosh 2014). In the next section, we will provide a brief recap of the factors that can affect the tACS-induced effects on cognitive functioning.

Factors Affecting TACS Effects

Like tDCS, see Chapter "Transcranial Direct Current Stimulation", tACS-induced physiological and behavioral effects are likely to depend on a large number of factors, such as for example electrode montage, stimulation frequency, and duration of the stimulation (Krause and Cohen Kadosh 2014). These factors need to be considered in order to reach the optimal enhancing effect of the desired cognitive functions. Methodological studies may augment our knowledge about these factors considerably. For instance, computational modeling approaches can help to shed light about the optimal combination of stimulation parameters, and can offer important insight into the effects of different electrode montages (Iacono et al. 2015; Neuling et al. 2012; Paulus 2011), although more research is still needed to optimize and physiologically validate these models. Moreover, combining tACS with EEG and/or MEG measurements can further elucidate the mechanisms of action of tACS.

Electrode Montage

Likewise tDCS, tACS needs at least two electrodes to work: a target electrode, which is placed over the brain area of interest, and a reference or return electrode, which is positioned over another region (either cephalic or extracephalic). When the return electrode is placed on the scalp, it is typically positioned over a cortical region that is believed not to play any functional role in the experimental paradigm (Ruffini et al. 2014), and/or in some occasions its size is enlarged to make the area beneath the return electrode functionally inert (Nitsche et al. 2007). Current density modeling studies, however, have suggested that the position of the return electrode is critical in determining the electrical field distribution across the cortex as well as the electrical field distribution under the target electrode (Bikson et al. 2010). Therefore, as the effects of tACS result from the electrical polarization of neurons that are aligned with the applied field (Radman et al. 2009), the position of the return electrode is likely to be of critical importance. Empirical evidence supporting the critical role of the position of the return electrode comes from a recent study by Mehta et al. (2015). In this study, the left primary motor cortex was stimulated while varying the position of return electrode between four locations, two cephalic (fronto-orbital and contralateral primary motor cortex) and two extracephalic (ipsilateral and contralateral shoulder). Results confirmed that tACS-induced behavioral effects are critically dependent on the position of the return electrode, as only the montage with extracephalic return electrode contralateral to the target electrode was found to be effective in entraining physiological tremor.

Stimulation Frequency

Undoubtedly, stimulation frequency is a factor playing a crucial role in mediating tACS effects. It is often assumed that tACS entrains endogenous oscillations to the stimulation frequency (Battleday et al. 2014; Helfrich et al. 2014a). An already earlier mentioned in vitro study showed that tACS enhances endogenous oscillatory activity only when the applied stimulation matched the endogenous frequency (Schmidt et al. 2014). Moreover, whenever the cortical slice did not have an endogenous frequency, neuronal activity entrained to all tACS frequencies. This indicates that the endogenous oscillations constrain the effect of tACS to frequencies that match them. To effectively target neuronal oscillatory activity, the stimulation frequency should thus be adapted to the frequency that matches spontaneous dominant EEG activity and that it is assumed to correlate with the specific cognitive function of interest—an assumption that has received empirical support from several recent studies (Kanai et al. 2008; Voss et al. 2014; Lustenberger et al. 2015; Cabral-Calderin et al. 2015; Janik et al. 2015; Schaal et al. 2015). Importantly, as endogenous cortical rhythms vary interindividually (e.g., Pollock et al. 1991; Stassen et al. 1987), it is reasonable to assume that tACS may be more effective when applied at the individual endogenous frequency—again, an assumption that has received considerable support (e.g., Cecere et al. 2015).

This makes it necessary to assess individual endogenous frequency via EEG or MEG measurements, to tailor tACS frequency to the individual needs.

Stimulation Duration

The duration of the stimulation instead seems to be critically related to the likelihood of observing tACS after-effects. For instance, Strüber et al. (2015) tested the relationship between stimulation duration and the likelihood to observe tACS after-effects. They showed that alpha tACS applied intermittently for 1 s duration did not elicit any after-effects on EEG amplitude and phase, which were instead observed in a previous study with identical parameters in terms of intensity and electrode montage, but longer (i.e., 20 min) stimulation duration (Neuling et al. 2013). These results confirmed that stimulation duration is a critical factor for eliciting tACS after-effects, and can explain why no tACS after-effects have been observed in animal studies so far, which typically use stimulation protocols in the range of seconds (for a review, see Reato et al. 2013). More importantly, these results corroborate the hypothesis that tACS after-effects are due to changes in synaptic plasticity, which are unlikely to occur with too short stimulation durations. Consistent evidence supporting the notion that tACS after-effects reflect plastic changes rather than entrainment comes from another recent study by Vossen et al. (2015). The authors applied repeated tACS at individual alpha frequency. Stimulation intervals were manipulated, so that the follow-up stimulation was either in phase (continuous condition) or out of phase (discontinuous condition) in relation to the previous stimulation. After-effects (i.e., enhanced EEG alpha amplitude) were found regardless of the continuous versus discontinuous condition. This challenges the assumption that after-effects are due to entrainment, based on which only the continuous condition should have produced after-effects. Moreover, consistent with the results of Strüber et al. (2015), tACS after-effects were observed only for intermittent protocols of 8 s stimulation duration, but not for the shorter (i.e., 3 s) stimulation duration. Taken together, the findings of Strüber et al. (2015) and Vossen et al. (2015) support the idea that synaptic plasticity and not entrainment is the key factor responsible for tACS after-effects. However, more research is needed to confirm that such short stimulation protocols can in fact induce plasticity.

Conclusion

tACS has the potential to enhance cognitive functioning by modulating rhythmic cortical activity within and between cortical areas. tACS seems to be more effective when applied at the individual endogenous frequency pointing to the necessity to tailor tACS frequency to the individual needs. In particular, theta tACS seems to support WM performance, whereas beta tACS sustains motor learning, and alpha and gamma tACS are more related to visual perception and creativity.

However, much more research has to be done to improve our knowledge about the enhancing effects of tACS on cognition and how to optimize stimulation protocols (e.g., intensity and duration of the stimulation, electrode size and number, scalp placement). It is important to acknowledge that extensive research is needed to verify whether the observed tACS-enhanced cognitive effects are preserved over time. Previous studies have shown that repetitive sessions of tDCS can increase the effects of stimulation (Nitsche and Paulus 2011), but it remains to be established whether the same applies to tACS. Hence, future studies assessing the impact of multiple stimulation sessions and the risk of incurring potential side-effects are necessary. Although more research is needed to fully understand the effects tACS exert on cognition at long term, we conclude that, tACS is a promising tool for enhancing cognitive functions.

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